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The **American Ornithologists' Union** will offer several **Marcia Brady Tucker Travel Awards** to help defray expenses of outstanding students wishing to present a lecture or poster paper at the society's meeting in Pittsburgh. The paper may have multiple authors (not true for best student paper competition; see Call for Papers) but the student's name must be first and the student must present the paper/poster. **Beginning in 1989, no student shall receive more than one MBT Travel Award**; students who have received one past award will be eligible for one more. To apply, send the following material to **Robert M. Zink, Museum of Natural Science, Louisiana State University, Baton Rouge, LA 70803, USA** by **15 May 1989**: (1) expanded abstract of paper, maximum 3 typed double-spaced pages, to include methods, major results, and scientific significance (i.e. not "results will be discussed . . ."; (2) curriculum vitae; (3) anticipated budget of **only travel expenses**; (4) letter of support mailed separately from the academic advisor supervising the research. Note that **10 copies of all materials (except reference letter) must accompany each application.** Applications for MBT awards do not guarantee a place on the scientific program; see instructions given with the Call for Papers in the meeting announcement. Students are expected to present their papers, irrespective of a travel award, if granted a place on the scientific program. Recipients of any A.O.U. research awards during 1989 cannot be considered for MBT funding. The MBT Travel Award competition is separate from competition for best student paper/poster awards (see Call for Papers for rules).

The **20th International Ornithological Congress** will take place in Christchurch, **New Zealand**, on **2-9 December 1990**. The Congress program will include 7 plenary lectures, 48 symposia, contributed papers (spoken and poster), workshops, round-table discussions, and films. There will be a mid-Congress excursion day. Longer tours are planned to interesting ornithological sites in New Zealand before and after the Congress, including the post-Congress cruises to sub-antarctic islands.

The second and final **Circular of the Congress** will be available after 1 October 1989 and will include the registration papers and forms for submitted papers. New Zealand will also host the **20th World Conference of the International Council for Bird Preservation** in Hamilton on **21-27 November 1990** and a **Pacific Festival of Nature Films**, in Dunedin on **27 November** to **1 December 1990**.

Requests for the final circular, which includes information on the above events, should be sent to **Ben D. Bell, Secretary-General, 20th International Ornithological Congress, School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand** (Telex: NZ30882 VUWLIB; Facsimile: NZ 64-4-712070).

GROWTH AND ENERGETICS OF ARCTIC TERN CHICKS (*STERNA PARADISAEA*)

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ABSTRACT.—We studied energy requirements of Arctic Tern chicks (*Sterna paradisaea*) in Ny Ålesund, Svalbard (79°N, 12°W) with special emphasis on thermoregulatory and activity costs. We used doubly labeled water to estimate energy expenditure in the field (E_{dlw}) and made laboratory measurements of the different components of total energy requirement (E_{req}). Comparison of DLW-estimates with oxygen consumption measurements showed that E_{dlw} underestimated total energy expenditure 4.5–16.0% depending on the duration of the experiment. This was probably due to incorporation of isotopes in newly synthesized tissue. Field estimates of total energy expenditure from E_{dlw} were corrected accordingly. A tern chick model was used to measure operative temperature (T_e). At midday T_e reached values up to 20°C above ambient temperature (T_a) which ranged from 3.4–9.0°C. Based on the field estimates of E_{dlw} and T_e and the laboratory measurements of basal metabolic rate and thermal conductance, we conclude that there was a considerable energy saving (456 kJ = 26% of E_{req}) during the first 10–11 days of life, due to parental brooding. After this period, when the parents stop brooding, the energy required for thermoregulation accounted for only 16% of E_{req}. From 10 days after hatching onwards, the energy needed for activity increased considerably, up to 50% of E_{req} just before fledging (Day 20). Comparison of the energy budgets of Arctic Tern chicks with the more southerly occurring closely related Common Tern (*S. hirundo*; Ricklefs and White 1981) revealed only a slightly higher energy expenditure in the Arctic Tern chicks.
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ENERGY expenditure of chicks living in arctic and antarctic environments has been considered to be dominated by the costs for thermoregulation. Many physiologists have focused on the ability of chicks to cope with low environmental temperatures (e.g. Maher 1964, Norton 1973, Aulie and Steen 1976, Boggs et al. 1977, Pedersen and Steen 1979, Bech et al. 1984, Jørgensen and Blix 1985, Taylor 1985, Boersma 1986). However, the abiotic environment of chicks at high latitudes and the contribution of thermoregulatory costs to their total energy expenditure have not been quantified precisely. In addition to estimating thermoregulatory costs in relation to other energy requiring processes, interspecific comparison of closely related species from different latitudes should provide a better understanding of the influence of the polar environment on chick energy requirements.

We studied energy requirements of Arctic Tern (*Sterna paradisaea*) chicks in the Arctic throughout the period from hatching to fledging, with special emphasis on thermoregulatory costs. We measured field growth, operative temperature, and total energy expenditure using doubly labeled water. In addition we analyzed carcasses and measured oxygen consumption in relation to ambient temperature in chicks of different ages. From this we estimated the costs of basal metabolism, growth, thermoregulation, activity, and total energy requirements, which were compared with the Common Tern (*S. hirundo*) and the Sooty Tern (*S. fuscata*; Ricklefs and White 1981).

METHODS

We studied Arctic Tern chicks in Ny Ålesund, Svalbard (79°N, 12°W) from 12 July to 6 August 1986. The breeding biology of the Arctic Terns in Ny Ålesund has been described by Bengtson (1971) and Lemmetyinen (1972).

The colony was visited regularly and individually marked chicks of known age were weighed with a Pesola spring balance. Wing length was measured

with a ruler to the nearest mm, and tarsus and head length with a flexible ruler to 0.1 mm.

We determined body composition in 11 chicks that ranged in age from 0 to 20 days, and in 2 adult birds. If the age of the chicks was not known from hatching records, body mass and total head length were used to estimate the age from the field measurements obtained in the colony. After collection, the carcasses were weighed immediately and deep-frozen. The carcasses were analyzed for water, lipid and nonlipid dry matter content at the Department of Zoology of the University of Trondheim. We dried the carcasses at 70°C to constant weight and lipids were extracted in petroleum ether. The energy density of individual birds was calculated using energy equivalents of 38 kJ/g lipid and 20 kJ/g nonlipid dry matter (Ricklefs 1974).

Weather data were obtained from the meteorological station in Ny Ålesund. To estimate the combined effect of ambient temperature, wind exposure, and solar radiation, we measured the operative temperature (T_e) which is the temperature a chick would attain if it lacked metabolic heat production and water loss (Bakken 1976). We measured operative temperature as the core temperature (copper-constantan thermocouple) of a tin cast covered with the pelt of a 1-day-old Arctic Tern chick. This mannequin was positioned in the typical microhabitat for a resting chick, which was a gravel field with patchily distributed vegetation not exceeding 10 cm in height. Operative temperature was recorded hourly with a Leeds and Northrup Speedomax recorder during 423 out of 576 hours of investigation, of which 384 hours formed 16 complete days. The operative temperature measurements were used to extrapolate from metabolism chamber conditions to the natural habitat for all age classes, because size apparently has a negligible effect on T_e (Chappell et al. 1984, Walsberg and Weathers 1986), and the color of the chicks changes only little during development until fledging.

In the laboratory we measured oxygen consumption of postabsorptive chicks ($n = 48$) at temperatures ranging from 0 to 37°C (for methods, see Klaassen et al. 1989). Oxygen consumption was converted to energy expenditure using 20 kJ/l O_2 assuming fat metabolism. Basal metabolic rate (BMR) and thermal conductance (h) of the chicks are described as functions of body mass (M, g):

$$\text{BMR} = 0.60 + 0.029\text{M} - 0.00023\text{M}^2 \text{ kJ}\cdot\text{g}^{-1}\cdot\text{day}^{-1} \quad (1)$$

$$h = 0.58\text{M}^{-0.486} \text{ kJ}\cdot\text{g}^{-1}\cdot\text{day}^{-1}\cdot{}^{\circ}\text{C}^{-1} \quad (2)$$

(Klaassen et al. 1988). We calculated daily thermoregulatory costs (E_{th}) in the field from operative temperature and body mass using Eqs. 1 and 2:

$$E_{th} = h(T_b - T_e) - \text{BMR kJ}\cdot\text{g}^{-1}\cdot\text{day}^{-1} \quad (3)$$

if $h(T_b - T_e) > \text{BMR}$, where T_b is body temperature (39°C; Klaassen et al. 1989). If $h(T_b - T_e) \leq \text{BMR}$, E_{th} was assumed to be 0 kJ·g^{-1}·day^{-1}.

In the field CO_2 production was measured with doubly labeled water (DLW; Lifson and McClintock 1966, Nagy 1980). We injected 10 chicks that varied in age between 0 and 19 days with 0.14 to 0.19 ml of a mixture containing 44% of 99.84 atoms% D_2O and 56% of 90.23 atoms% $H_2{}^{18}O$. The amount depended on the size of the bird. A 15-μl blood sample was taken before injection, 3 h after injection (when equilibration was assumed to be complete) and every subsequent 12 h during the following 36 h. In two cases the injected chicks were not recaptured after 3 h, but were sampled 12 h after injection. Blood samples were taken from a neck vein in chicks up to 4-days-old, and from a wing vein in older chicks. Samples were sealed in a glass microcapillary. It took ca. 20 min to catch, weigh, measure, bleed, and release chicks. Blood samples were stored at 5°C until analyses by Isotope Ratio Mass Spectrometry (Masman and Klaassen 1987) at the Center of Isotope Research (C.I.O.) in Groningen.

Validation of the DLW method was obtained on three chicks of different ages, which we transported from Svalbard to Trondheim. We followed the same procedure as in the field, but between the blood samplings we measured oxygen consumption in an open flow system. Air was sucked through a 9 or 17 l metabolic chamber with a flow rate of approximately 1 l/min. The air was dried over silica-gel and oxygen concentration was determined with a Servomex 1100A oxygen analyzer. Ambient temperature in the chamber varied between 3 and 30°C. The chicks were fed *ad libitum* with fresh Torsk (*Brosme brosme*). Oxygen consumption was calculated according to Hill (1972) and converted to CO_2 production with a RQ of 0.73 as the diet consisted mainly of protein and fat.

We assumed linear mass changes in the chicks, and calculated CO_2 production from ^{18}O and D enrichments in the blood samples with eq. 21 of Lifson and McClintock (1966), which was adapted for physical fractionation effects (Lifson and Lee 1961, Lifson and McClintock 1966). Body water was calculated on the basis of the carcass analyses results. To obtain two independent estimates of CO_2 production over ca. 24 h per chick, we used each blood sample analysis only once. We calculated CO_2 production for the interval between the first and third and between the second and fourth sample after injection. In 4 cases the fourth blood sample was too low in ^{18}O to allow accurate calculation of the CO_2 production. This gave 16 independent CO_2 production estimates in 10 chicks of different ages. Carbon dioxide production was converted to total energy expenditure (E_{dlw}) using an equivalent of 25 kJ/l CO_2.

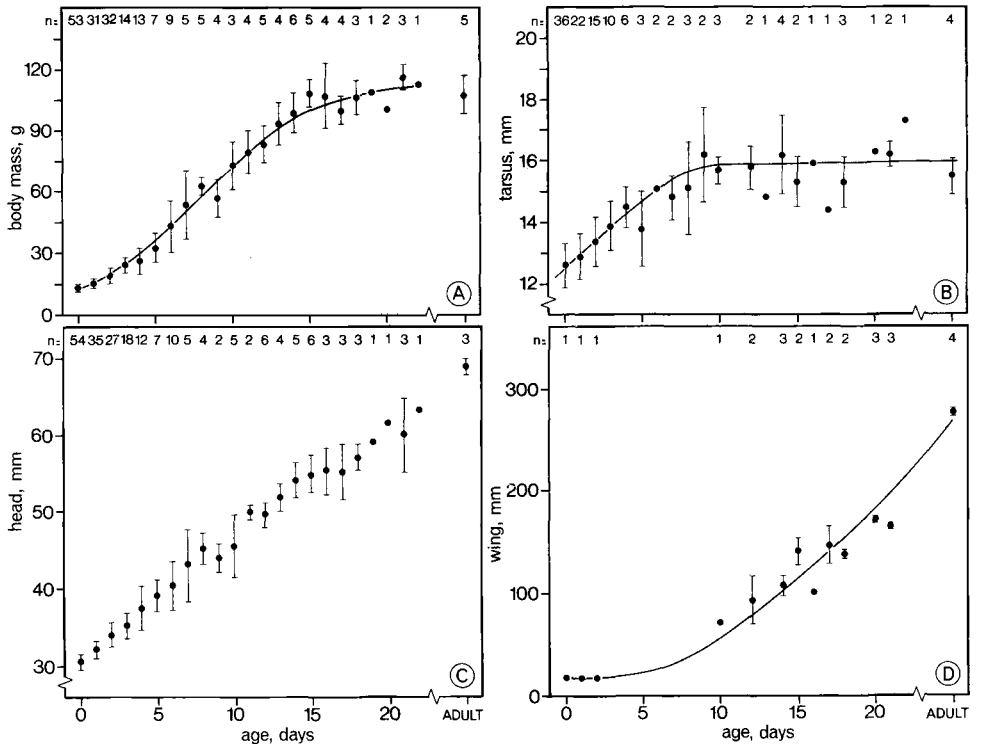

Fig. 1. Development of body mass (A), tarsus length (B), head length (C), and wing length (D) as a function of age in Arctic Tern chicks. Measurements on adults are included for comparison. The line in (A) was calculated (Eq. 4), whereas the lines in (B) and (D) were fitted by eye.

RESULTS

The increase of body mass with age (t, days) (Fig. 1A) was fitted to a logistic equation (Ricklefs 1967):

$$M = 115/(1 + 8.0e^{-0.263t})\ g \qquad (4)$$

The tarsus had a high growth rate from hatching until Day 7 when it had nearly reached adult length (Fig. 1B). Head length increased nearly linearly with age (Fig. 1C). In contrast, the wing only grew rapidly after Day 5 to Day 8, and reached 60% of adult length at fledging around Day 22 (Fig. 1D).

The carcass analyses enabled us to convert body mass gain to energy deposition and to estimate total body water content, necessary for the calculations of CO_2 production from the isotope enrichments in the blood samples. Body water content (C_w) decreased with age (Fig. 2A) following the expected pattern (Ricklefs 1974) and was described by the equation:

$$C_w = 84.6(t + 1)^{-0.091}\% \qquad (5)$$

($r = -0.875$, $P < 0.001$). The amounts of lipid and nonlipid dry mass (Fig. 2B) were accumulated with a nearly constant ratio from the third day of age onwards. About 28% of the water-free tissue was lipids. As a consequence, the increase of energy density of body tissue (C_{et}) with age (Fig. 2C) was mainly due to the decrease in water content. This increase in energy content was described by:

$$C_{et} = 3.65(t + 1)^{0.306}\ kJ/g\ wet \qquad (6)$$

($r = 0.929$, $P < 0.001$). From the growth curve (Eq. 4) and the relationship for energy density of body tissue with age (Eq. 6), we calculated the daily cost for tissue deposition (E_{tis}). Assuming a synthesis efficiency of 75% (Ricklefs 1974), the costs for biosynthesis (E_{syn}) were derived by $E_{syn} = E_{tis}0.33$ kJ/day.

We estimated the costs for thermoregulation in the field by using the information of the

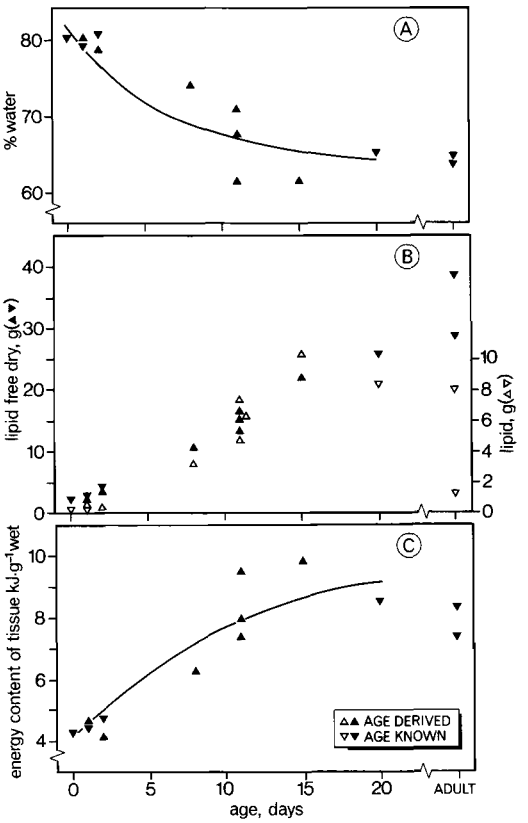

Fig. 2. Water content as percentage of total body mass (A), lipid mass (B), lipid-free dry mass (B), and energy content (C) of 11 Arctic Tern chicks and 2 adults as a function of age.

actual thermal environment, measured as T_e, and the relation between T_a and oxygen consumption established in the laboratory (Klaassen et al. 1989). Ambient temperatures in Ny Ålesund were relatively stable and ranged between 3.4 and 9.0°C over the investigation period. In contrast, the operative temperature varied considerably. On cloudy days with low solar radiation the operative temperature was slightly elevated above the ambient temperature; but on clear days, operative temperature could reach values of up to 29°C (Fig. 3). The daily mass specific thermoregulatory cost was calculated from Eqs. 1-4, and assumed no brooding by the parents and a body temperature of 39°C maintained by the chicks (Klaassen et al. 1989). Mass specific thermoregulatory costs decreased rapidly over the first 7 days. From an age of ca. 10 days onwards, thermoregulatory costs stabilized around 0.6 $kJ \cdot g^{-1} \cdot day^{-1}$ (Fig. 4).

Total energy expenditure of the chicks, including basal metabolism, biosynthetic and thermoregulatory costs as well as costs for activity, was estimated by DLW. Carbon dioxide production by chicks, calculated from the measured oxygen consumption by indirect calorimetry, was systematically higher than measured by DLW (Table 1). This underestimation of the metabolic rate using DLW was less pronounced in the first (samples 1 and 3) than in the second (samples 2 and 4) part of the experiment. The errors were −4.5% (SD = 2.4) and −16.0% (SD = 9.0) for the first and second part, respectively. The field estimates of CO_2 production from DLW showed the same relatively low values for experiments started half a day after injection of the isotopes (Table 2). After correcting for the underestimations, the total energy expenditure in the field (Fig. 5) was described by:

$$E_{dlw} = 9.70(t + 1)^{1.170} \text{ kJ/day} \qquad (7)$$

($r = 0.988$, $n = 16$, $P < 0.001$).

The costs of activity (E_{act}) were calculated by subtraction of basal metabolic, biosynthetic and thermoregulatory costs from the total energy expenditure as measured with DLW.

We reconstructed total energy requirements

TABLE 1. Validation of the doubly labeled water technique. Comparison of CO_2 production estimates from doubly labeled water experiments and indirect calorimetry.

Individual	Age (days)	Initial mass (g)	Mass gain (g)	CO_2 production (mmol/day) DLW	CO_2 production (mmol/day) Indirect calorimetry	Error (%) DLW
544	5.5	41.0	6.2	151	159	−5.0
544	6.0	42.6	5.5	128	173	−26.0[a]
521	13.0	74.0	8.2	303	309	−2.0
521	13.5	69.4	16.5	289	334	−13.5[a]
502	19.0	109.0	−1.6	283	303	−6.6
502	19.5	108.0	−5.1	267	292	−8.6[a]

[a] Carbon dioxide production calculated over the second part of the experiment, see text.

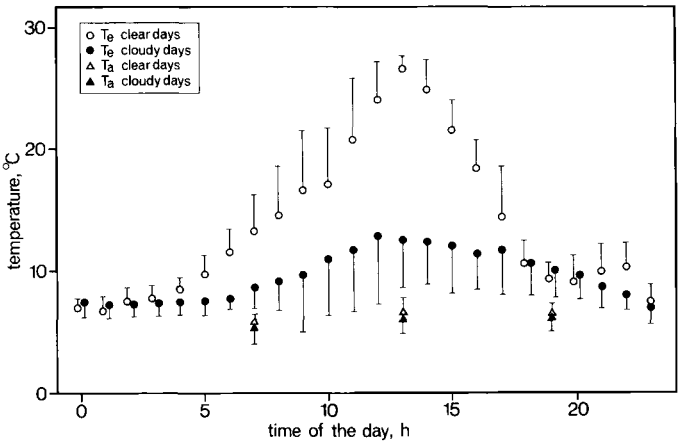

Fig. 3. Daily ambient and operative temperature (±SD) for clear (cloud cover ≤ 4/8) and cloudy (cloud cover > 4/8) days, at the Arctic Tern colony in Ny Ålesund, Svalbard, between 12 July and 6 August 1986.

(E_{req}) of Arctic Tern chicks as a function of age by integrating the data on energy costs of basal metabolism, biosynthesis, thermoregulation, activity, total energy expenditure and tissue deposition (Fig. 6).

The complete separation of BMR and costs for biosynthesis in young chicks was not possible. Hatchlings which still contain yolk, even when they are starved before BMR measurement, continue tissue growth, using the yolk as a source for metabolites (Klaassen et al. 1987). Because it is unclear whether all synthetic costs are included in the "hatchling" BMR, the difference between total energy expenditure as measured by DLW and BMR during the first 3 days of age was assumed to consist of additional costs for synthesis in nonstarved hatchlings.

A second complication in reconstruction of the energy budget was that during the first 11 days, total energy expenditure (as calculated by the summation of BMR, synthesis, and thermoregulation) exceeded the energy expenditure estimated by DLW. This overestimate of 456 kJ or 26% of E_{req} was at least partly due to excluding the brooding behavior of the parents from the energy budget. During the first week after hatch, the chicks were thermolabile

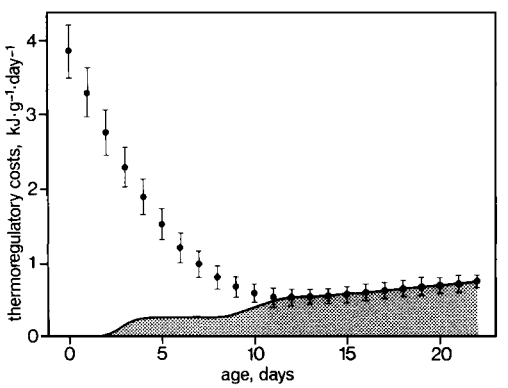

Fig. 4. Thermoregulatory costs as a function of age, calculated from operational temperature and laboratory-established relations between temperature and oxygen consumption. Indicated variation (±SD) expresses variation in measured operative temperatures (see Fig. 3). Shaded area represents the estimated actual thermoregulatory costs after accounting for parental brooding (see text).

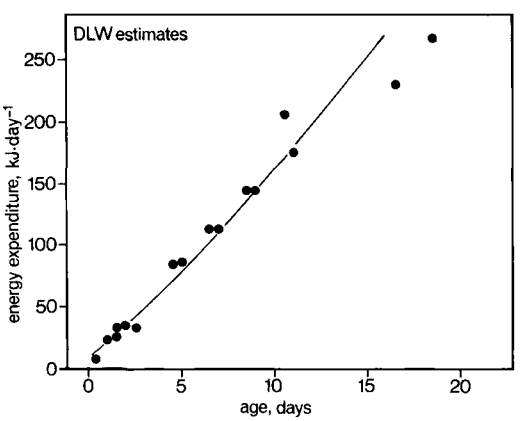

Fig. 5. Total energy expenditure measured with doubly labeled water, of free-living Arctic Tern chicks as a function of age. The corrected values are plotted (see Table 2).

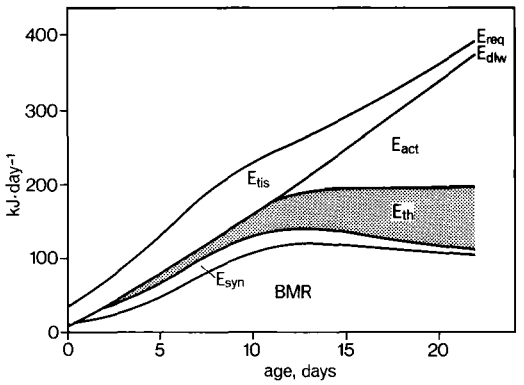

Fig. 6. Total energy requirements (E_{req}) of free-living Arctic Tern chicks in Ny Ålesund, Svalbard, from hatching until fledging. Total energy expenditure measured by DLW (E_{dlw}) is partitioned in BMR, tissue synthesis (E_{syn}), thermoregulation (E_{th}), and costs for activity (E_{act}). The accumulation of body tissue (E_{tis}) completes the total energy requirements.

TABLE 2. Field estimates of CO_2 production with doubly labeled water.

Individual	Age (days)	Initial mass (g)	Mass gain (g)	CO_2 production (mmol/day) Uncorrected	CO_2 production (mmol/day) Corrected[b]
12	0.5	12.7	3.8	22	23
12	1.0	15.1	1.5	36[a]	43
89	1.5	16.5	4.5	56	59
79	1.5	14.4	0.0	45	47
79	2.0	14.3	0.3	53[a]	63
1	2.5	17.9	2.0	48[a]	57
120	4.5	35.0	12.0	147	154
120	5.0	45.3	13.5	131[a]	156
86	6.5	45.2	5.3	192	201
86	7.0	48.5	12.0	170[a]	202
58	8.5	61.9	8.6	245	257
58	9.0	64.5	8.5	213[a]	254
56	10.5	81.0	1.0	349	365
56	11.0	80.0	4.0	261[a]	311
86	16.5	97.0	6.0	342[a]	407
58	18.5	109.0	3.0	453	474

[a] Carbon dioxide production calculated over the second part of the experiment, see text.

[b] Corrected according to the estimated errors for first and second part of DLW experiment, as determined in validation experiment.

(Klaassen et al. 1989) and were nearly continuously brooded by the parents (Busse 1983). In the second and third week after hatch, the parents may still brood or shelter their chicks, at least during periods of rain (Busse 1983). The thermal model is static, and not capable of selecting the most favorable microenvironment. Although we aimed for the most favorable site for our measurement, this technique probably underestimated the actual T_e encountered by chicks in the field even when not brooded by the parents. Therefore, during the first week, thermoregulatory costs were assumed to be close to zero, and increased only gradually until Day 11 (Figs. 4, 6).

The calculated energy budget of Arctic Tern chicks reveals that total energy requirements over the first 21 days of age amount to 4,442 kJ/chick. Of the total energy requirements 42% is allocated to basal metabolism, 8% to biosynthesis, 18% to thermoregulation, 9% to activity, and 23% to tissue deposition.

DISCUSSION

The use of DLW in rapidly growing animals may lead to severe errors in estimates of total energy expenditure, due to irreversible and disproportional incorporation of the isotopes in body tissue (Nagy 1980, Williams and Nagy 1985), although the method has been used widely (Fiala and Congdon 1983, Williams and Nagy 1985, Williams and Prints 1986). Williams and Nagy (1985) argued that an underestimate of CO_2 production measured by DLW resulted from the incorporation of hydrogen but not oxygen into newly synthesized tissue. Assuming the "worst case" scenario for the Savannah Sparrow nestlings (*Passerculus sandwichensis*), Williams and Nagy (1985) calculated a possible underestimate of E_{dlw} by 25%. In the Arctic Tern chicks, measured error was up to −16.0% and well outside the range of ±8% generally found in validation experiments in animals with fairly stable body mass (Masman and Klaassen 1987). Carbon dioxide production measurements showed that during the experiment the underestimation became more pronounced. This suggests an increasing incorporation rate of deuterium during the experiment. In the absence of more detailed studies we assume our procedure and corrections are valid.

The total energy requirements of Arctic Tern chicks changed dramatically during the second week. At this point the tarsus was virtually full grown (Fig. 1B), which indicates advanced locomotory capacity. This was confirmed by the contribution of activity costs to the total energy expenditure at Day 11. Furthermore, chicks were capable of thermoregulation at fairly low costs.

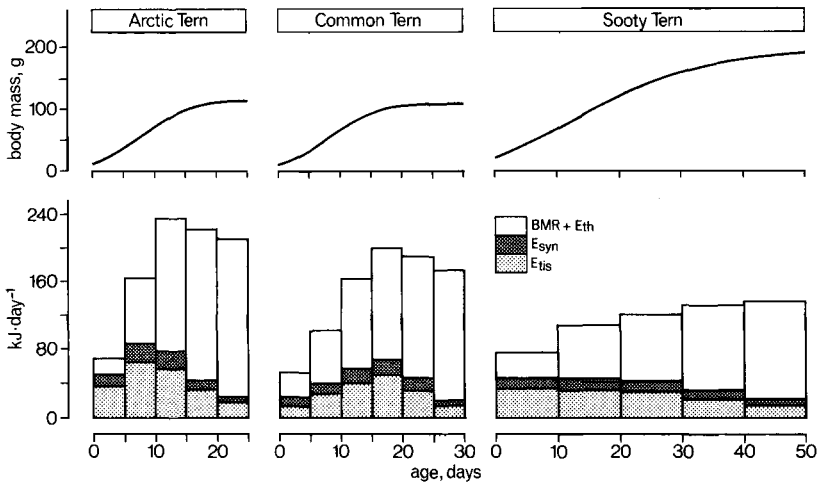

Fig. 7. Growth curves and energy requirements of Arctic, Common, and Sooty terns. Energy requirements were compiled from costs for tissue accumulation (E_{tis}), tissue synthesis (E_{syn}), and basal metabolism plus thermoregulation (BMR + E_{th}). Energy requirements for activity are excluded.

The favorable development of both locomotory and thermoregulatory capacities reduced the need of parental attention, and left more time for the parents to forage. This change occurred when the chick had reached half of its maximum energy requirement level. For the chick, these changes might be considered as a change from an altricial to a more precocial mode of life.

To evaluate the effect of the arctic environment on total energy requirements, we compared the Arctic Tern chick energy budget with the budgets of two related species studied at different latitudes (Fig. 7). Common Terns were studied on Great Gull Island, New York (41°N, 74°W), and the Sooty Terns on Bush Key, Dry Tortugas, Florida (25°N, 81°W; Ricklefs and White 1981). Activity costs were excluded from the comparison as they are unavailable for the Common and Sooty tern. Arctic and Common tern grow rapidly and have similar growth curves. The patterns of energy requirements as a function of age are also similar. Energy expenditure and deposition increase through the midpoint of development when, because of reduced tissue accumulation, they decrease slightly. The Sooty Tern grows slowly, with continuously low daily energy requirements during development.

Ambient temperatures on Great Gull Island and Bush Key were 25°C and 35°C during the day, and 17°C and 27°C during the night, respectively. Therefore, we assumed thermoregulatory costs were lower for both Common and Sooty tern chicks. The difference between energy requirements of Common and Arctic tern chicks was mainly a result of the differences in thermoregulatory costs, which never exceeded 0.73 times BMR or 21% of the total energy requirements in Arctic Tern chicks. The values of 21% and 18% of E_{req} for maximum and mean thermoregulatory costs may be slightly higher than the actual values because of underestimation of T_e (see above), and the possible effect of endogenous heat production during activity on thermoregulation. The heat increment of feeding did not substitute for thermoregulatory costs in Arctic Tern chicks (Klaassen et al. 1989).

In the Arctic Tern chick, there appear to be mechanisms to reduce thermoregulatory requirements. Fat content in Arctic Tern chicks was high (about 28% of wet body mass) compared to Common and Sooty tern chicks (about 22%; Ricklefs and White 1981). Fat reserves might increase insulation and serve as an energy reserve during periods of bad weather. A high metabolic capacity would also be beneficial in arctic environments to ensure enough endogenous heat production capacity for thermoregulation. The basal metabolic rate might indicate the metabolic capacity, and BMR in Arctic Tern hatchlings is indeed relatively high compared with relatives from lower latitudes (Klaassen et al. 1989).

Thus Arctic Tern chicks seem to be well prepared for the "cold Arctic" at relatively low extra expenses. However, the energy budgets used for the comparison (Fig. 7) do not cover all costs. Complete partitioning of the total energy requirements can elucidate life history strategies in related species that reproduce at different latitudes.

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The **Frank M. Chapman Memorial Fund** gives grants in aid of ornithological research and also postdoctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. **Applications are reviewed once a year and must be submitted no later than 15 January, with all supporting material.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA.**

There were no Chapman Fellowships awarded for 1988.

Chapman grants for 1988, totaling $43,954.00, with a mean of $698.00, were awarded to: Juan Amat, moulting ecology of the Red-crested Pochard (*Netta rufina*) in Spain; Gonzalo Arango, la taxonomia y las distribucion del genero *Thamnophilus* en Colombia; Todd W. Arnold, proximate and ultimate constraints on clutch size in American Coots; John M. Bates, winter survivorship in the House Sparrow (*Passer domesticus*): a morphologic and allozymic perspective; Douglas A. Bell, hybridization between the Western Gull and the Glaucous-winged Gull; William L. Benner, range expansion and rapid evolution in the House Finch *Carpodacus mexicanus*; Robert E. Bleiweiss, biochemical systematics of hummingbirds using DNA-DNA hybridization; William I. Boarman, environmental components of selection on avian song; Rhys V. Bowen, evolutionary significance of interspecific foraging competition; Reed Bowman, mediation of asynchronous hatching and brood reduction in White-crowned Pigeons; James V. Briskie, dynamics and consequences of copulation patterns in Smith's Longspur; Neil J. Buckley, role of information transfer in the foraging behavior of Turkey Vultures *Cathartes aura*; Carolee Caffrey, cooperative breeding in American Crows: do helpers help?; Angelo P. Capparella, genetic differentiation among Patagonian birds in secondary contact; Jose Maria Cardosa da Silva, taxonomic studies of birds collected in Urucum and Corumba, Brazil; Kevin Cash, brood reduction in Swainson's Hawk; Glen Chilton, discrimination of dialects by female White-crowned Sparrows; Carla Cicero, variation in the song of the Lincoln's Sparrow (*Melospiza lincolnii*) in California; Thomas Peter Coombs-Hahn, environmental control of reproductive physiology in the Red Crossbill; Donald A. Croll, diving and energetics of the Murre; Timothy Crowe, systematics of Galliformes, Raptors, Bustards and Larks; Robert W. Dickerman, ornithological exploration of Upper Guinea lowland forest refuge; Katherine E. Duffy, the migration of owls at Cape May Point, New Jersey; David Enstrom, continuing investigation of delayed plumage maturation in Orchard Orioles; B. Patricia Escalante-Pilego, geographic variation in *Geothlypis* of Baja, California, and western Mexico; Mary C. Garvin, the role of blood parasites in mechanisms of avian sexual selection; Stephen M. Gatesy, a functional study of avian terrestrial locomotion; Rosemarie Gnam, breeding biology of the Bahama Amazon (*Amazona leucocephala bahamensis*); Pedro C. Gonzales, study of AMNH collection of Palawan birds; Martha Groom, detriments of nesting success and nest-site selection in four beach-nesting bird species; Percy N. Hebert, asynchronous hatching and parental investment in the Yellow Warbler (*Dendroica petechia*); Geoffrey E. Hill, female mate preference in relation to male carotenoid pigmentation in the House Finch; Sylvia Hope, geographic variation in call repertoire of the Steller's Jay; L. Scott Johnson, the function of territorial intrusions and mate guarding in House Wrens; Ian L. Jones, the evolution of social signals of the seabird genus *Aethia*; Michael C. Kaspari, experiments with overwintering mixed species flocks in the Sonoran Desert; Mary Katz, song variation in *Pardalotus striatus*, and its relationship to morphological variation; L. Henry Kermott, ectoparasitism of nestling House Wrens by *Protocalliphora braueri* (Diptera); Nedra Klein, geographic variation and systematics of the Yellow Warbler; Natasha B. Kotliar, a hierarchical concept of patchiness: implications for the foraging behavior of nectarivorous birds; David S. Lee, systematics of seabirds from North Carolina and the Philippines; Bruce Lyon, ecology and evolution of intraspecific brood parasitism in American Coots; Randall J. Mitchell, the effect of nectar rewards on hummingbird behavior and pollen deposition and dispersal; David C. Oren, avifauna of Maranhao State, Brazil; David Pashley, distribution of wood warblers in the Neotropics; A. Townsend Peterson, evolutionary relationships of the *Aphelocoma* Jays; Don Roberson, research on *Pterodroma* in AMNH collection; Frank G. Rozendaal, systematics of Asian-Pacific bush-warblers of the genera *Cettia, Urosphena, Tesia* and *Bradypterus* (Aves: Sylviidae); Karl-L. Schuchmann, behavior and reproduction biology of the Tooth-billed Hummingbird (*Androdon aequatorialis*); Gilles Seutin, mechanism of species

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GEOGRAPHIC VARIATION AND SEXUAL DIMORPHISM IN THE TREMBLERS (*CINCLOCERTHIA*) AND WHITE-BREASTED THRASHER (*RAMPHOCINCLUS*)

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ABSTRACT.—I compared interisland variation in color and in length of wing, tarsus, and bill of the Lesser Antillean thrashers, *Cinclocerthia* and *Ramphocinclus* (Mimidae). Statistical analyses show that some early-taken specimens were missexed. I recognize two species of trembler, *Cinclocerthia ruficauda* (Brown Trembler) and C. *gutturalis* (Gray Trembler), and one of *Ramphocinclus* (White-breasted Thrasher). Brown Tremblers from Saba to Monserrat ("*C. r. pavida*") are not considered separable from those of Guadeloupe (*C. r. tremula*).

I summarize foraging methods and give possible explanations for the smaller amount of sexual dimorphism in bill length in *Cinclocerthia* on islands where *Ramphocinclus* occurs.
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THE avifauna of the West Indies is rich and well-known. Yet it has been underused as a source of information for zoogeographic and evolutionary studies. The Lesser Antilles, which extend in an arc south from the Virgin Islands toward Trinidad, are home to several endemic genera, including the tremblers (*Cinclocerthia*) and the White-breasted Thrasher (*Ramphocinclus brachyurus*).

Tremblers are long-billed, reddish brown or brownish gray thrashers found from the islands of Saba and St. Eustatius south to St. Vincent. At present, they are found primarily in wet, upland forests and less frequently in second growth (Bond 1936, American Ornithologists' Union 1983). In earlier classifications (e.g. Ridgway 1907), the grayish forms on Martinique and St. Lucia were both considered separate species. Current arrangements (Hellmayr 1934, Davis and Miller 1960) classify all the tremblers as a single species with six subspecies. From north to south, these subspecies are *Cinclocerthia ruficauda pavida* (Saba, St. Eustatius, St. Kitts, Nevis, and Monserrat), *C. r. tremula* (Guadeloupe), *C. r. ruficauda* (Dominica), *C. r. gutturalis* (Martinique), *C. r. macrorhyncha* (St. Lucia), and *C. r. tenebrosa* (St. Vincent). For reasons given below, the grayish tremblers of Martinique and St. Lucia are here considered a separate species, *Cinclocerthia gutturalis* (the Gray Trembler), and the reddish brown birds of the other islands are considered to be *C. ruficauda*, (the Brown Trembler). A fossil trembler is also known from deposits between 2,500 and 4,500 Y.B.P. on the island of Antigua (Steadman et al. 1984, Pregill et al. 1988).

The two forms of the White-breasted Thrasher have been considered separate species (Ridgway 1907), but they are currently considered conspecific (Hellmayr 1934, Davis and Miller 1960). They inhabit the adjacent islands of Martinique (*Ramphocinclus brachyurus brachyurus*) and St. Lucia (*R. b. sanctaeluciae*). Thus *Ramphocinclus* is everywhere sympatric with *Cinclocerthia gutturalis* whereas *C. ruficauda* occurs alone both to the north and to the south of the islands on which *Ramphocinclus* and *Cinclocerthia* are sympatric.

MATERIALS AND METHODS

I noticed both long- and short-billed birds in most of the populations of tremblers in the collections of the American Museum of Natural History. This difference was at least in part correlated with sex; the long-billed birds were usually sexed as females, and the short-billed birds as males. Data from this and other museums showed that there were apparent exceptions, especially among the specimens from Dominica whence seven short-billed birds were sexed as females and four long-billed ones as males (nearly one-fourth of the early-taken, sexed specimens from that island). Other preliminary data suggested that sexual dimorphism was reduced on Martinique and especially St. Lucia, where *Ramphocinclus* occurs with *Cinclocerthia*, so I examined and measured most available specimens of these genera.

Of the 391 specimens examined, 359 adults (280 of *Cinclocerthia* and 79 of *Ramphocinclus*) were used in the

analyses. This is not a large sample by modern standards, but it is so much larger than the series available to earlier reviewers (Ridgway [1907] reported on 61 specimens, and Hellmayr [1934], on 50) that, for the first time, variation within several of the populations can be treated statistically.

Measurements taken included wing length (chord), tail length, tarsus length, length of bill from the anterior border of the nostril, and culmen from the junction of the bill with the skull. Of these, wing length and length of bill from nostril proved the most useful; tail length was so greatly affected by wear that many measurements of it were useless; and bill length from skull proved difficult to duplicate. The ratio of wing length to length of bill from nostril was calculated for each bird.

Before I attempted an analysis of the variation among the populations, it was necessary to establish the extent of sexual dimorphism in *Cinclocerthia.* Although Ridgway (1907) reported sexual dimorphism in bill length, I found long-billed birds sexed as males and short-billed birds as females. This raised the question of whether these birds were missexed or whether individual variation in this genus is unusually large.

Missexed birds are probably more numerous in collections than is generally realized. They can be detected most easily in species with little or no overlap in one or more measurements (e.g. grebes; Storer and Getty 1985, Storer 1987). Because the males of most bird species have longer bills than the females, collectors probably missex more individuals of species like the tremblers in which the reverse is true.

I used the largest sample, 99 adult specimens from Dominica, for preliminary tests. Thirty-six birds from that island collected by Albert Schwartz in 1961 and 1962 yielded the following data: bill from nostril—24 males, 20.1–22.3 mm; 10 females, 23.7–27.5 mm; wing length/bill from nostril—23 males, 4.16–4.86; 9 females, 3.25–4.01.

Assuming that these birds were correctly sexed, I compared these data with the measurements of all the earlier-taken birds. The bill lengths of four older specimens (22.4, 22.4, 22.6, 23.3 mm) fell above those for males and below those for females in the Schwartz series. Of these, all but the third were well within the range of wing/bill ratios (4.32, 4.35, 4.12, 4.23, respectively) for males in the Schwartz series. All except the first bird (which was unsexed) were sexed as males by the collectors. The third bird is nearer to Schwartz's males than to his females in both bill length and wing/bill ratio. Therefore, I considered all four to be males. Four birds sexed as males were within the range of females in both characters and nine "females" fell within the range of males. A tenth bird sexed as a female had a bill for which bill-from-nostril measurement could not be taken but had a total bill length that was within the range of males and outside the range of females. Therefore, I considered all 10 birds to have been missexed.

I believe the assumption that birds were missexed is valid. First, there is a decided gap between the data for males and females in Schwartz's sample, and second, 10 of the 14 presumably missexed specimens were taken by two collectors, A. Hyatt Verrill (7) and Selwyn Branch (3). (Two birds taken in 1905, presumably by Verrill, came to the University of Michigan Museum of Zoology by way of the collection of Henry K. Coale, who removed the original labels and substituted his own. It is possible that Coale may have switched the labels, assuming that the longer-billed bird was the male.) On the other hand, Bond's (1952) questioning or discrediting many of Verrill's bird records from Dominica suggests that he was not a careful worker.

The preliminary results were tested further by obtaining discriminant functions for wing length, tarsus length, and bill from nostril for the Schwartz sample and using these to test the remaining birds from Dominica. In all cases, the results from the preliminary analysis were confirmed by discriminant-function analysis. A similar analysis was performed on the birds from Guadeloupe. The results indicated that a single female (MCZ 66485) was missexed. However, the bill length was within the range of females and outside the range of males for that population, whereas the measurements for wing and tarsus were within the range of both sexes. Because dimorphism is greatest in bill length and because there were no other individuals showing overlap, this bird was considered correctly sexed as a female.

I also tested the sexing of tremblers from St. Lucia by using discriminant functions. A single bird (BM[NH] 94.1.2.242, collected in February 1893) sexed as a female was classified as a male by discriminant-function analysis and was, therefore, considered missexed. The sexes of other birds I assumed to have been missexed or that I sexed on the basis of measurements were verified by this test.

A preliminary discriminant-function test for the Dominica sample on birds from St. Vincent showed that two Schwartz birds from the latter island might have been missexed. Discriminant functions calculated from the St. Vincent birds not collected by Schwartz were used to check the Schwartz sample, and the likelihood of missexing was confirmed. The bill measurements of these two birds, sexed as males, fell within the range of females. These birds were taken in February, when gonads are small and the chance of missexing most likely, so they were considered missexed. The sexes assigned to birds unsexed by the collectors and to birds believed to have been missexed are listed in Appendix 1.

After sexing was checked and corrected, I calculated means and standard deviations for each sex of the population of trembler on each island. Descriptive statistics for three combination of islands were also calculated: those traditionally included in the race *pavida* (Saba through Monserrat), the islands of St.

Eustatius, St. Kitts, and Nevis (which were probably connected at times of lowered sea levels in the Pleistocene), and the islands included in *pavida* plus Guadeloupe. Pairwise comparisons (Sheffe tests) were used to determine the significance of interisland differences. Dimorphism indices for each character of each island population were calculated as the difference between the means for the sexes divided by the mean for the means of the sexes and multiplied by 100 (Storer 1966).

Because of the large overlap in measurements between the sexes in the White-breasted Thrasher, I did not attempt to check for missexed birds or to assign sex to those unsexed by the collectors. Means and standard deviations for the sexed birds in both populations were calculated, as was the mean for the means of the sexes of both this species and the Gray Trembler on the two islands where they are sympatric. The last were used to calculate a species index in the same way as the dimorphism index was calculated.

In *Cinclocerthia*, there was no statistically significant relationship between the distance between islands and the amount of difference between populations on adjacent islands (comparing mean measurements for wing length, tarsus length, and length of bill from nostril for each sex independently with the interisland distances using a correlation matrix). The analysis was simplified because the islands lie along what is essentially a single axis.

Similarly, I used a correlation matrix to test for a statistically significant relationship between island size and each of the three linear measurements. Again, no such relationship was found.

A discriminant-function analysis was used to predict the percentage of specimens that could be identified on the basis of the lengths of wing, tarsus, and bill from nostril. This was performed for pairs of islands by sex. Discriminant functions were calculated for the three measurements for each island pair. Individual specimens were scored by multiplying their measurements by these functions and summing the products. These scores, based on the linear functions of the three variables, were used to calculate the predicted range of scores for each island. Individual scores were compared with the predicted range of scores for each island, and the number of specimens correctly or incorrectly classified was expressed as a percentage. I tested Monserrat vs. Guadeloupe, Guadeloupe vs. Dominica, Guadeloupe vs. St. Vincent, Dominica vs. St. Vincent, and Martinique vs. St. Lucia. Because of their very different coloration, the gray forms on Martinique and St. Lucia were not tested against any of the rufous forms.

The series of specimens from the Schwartz Collection (now at the Museum of Natural History, Louisiana State University), plus a pair of the Martinique Gray Trembler from the Field Museum of Natural History, were compared for color differences by R. C. Banks, J. W. Fitzpatrick, T. R. Howell, N. K. Johnson, B. L. Monroe Jr., H. Ouellet, J. V. Remsen, and the author.

Results

There are no clear trends in measurements of *Cinclocerthia*, from north to south (Table 1), nor is there a color cline. Sexual dimorphism ranges from ca. 2–5% for wing and tail length, is less (0.4–3.3%) in tarsus length, and is large (12.8–19.6%) in length of bill from nostril. The last is greatest in the three northern races, least in *macrorhyncha*, and intermediate in the other two. The index for wing/bill-from-nostril ratio is also least in *macrorhyncha* because of the small dimorphism index in bill length.

In *Ramphocinclus*, the Martinique race (*brachyurus*) is consistently smaller than that on St. Lucia (*sanctaeluciae*), and, except in culmen length, considerably less dimorphic (Table 1).

Tremblers from Saba, St. Christopher, Nevis, and Monserrat ("*pavida*") did not differ consistently in color. Birds from Guadeloupe (*tremula*) reportedly are darker overall and have grayer, less tawny, chests than "*pavida*" (Ridgway 1907). Although Schwartz's series from Guadeloupe is, on average, slightly darker than his series of "*pavida*," there is great overlap in this character; and the color of the underparts, including the chest, is quite variable, with nearly complete overlap between the Guadeloupe birds and those from the islands to the north.

According to Ridgway (1907), birds from Guadeloupe are dark like those from St. Vincent (*tenebrosa*) and thus darker than birds from Dominica (*ruficauda*). While the birds from Guadeloupe average darker above than those from Dominica, there is considerable overlap; and there is a nearly complete overlap in the color of the underparts.

Birds from St. Vincent are the darkest of the rufous populations. They are sufficiently deeper rufous on the back and darker gray on the crown and nape than the birds from Dominica to warrant subspecific recognition. Below, the St. Vincent birds average darker and tend to be more heavily marked with broad, diffuse streaks, but there is considerable overlap between the two populations in these two characters.

The Gray Tremblers from Martinique (*gutturalis*) and St. Lucia (*macrorhyncha*) differ markedly in overall color from the Brown Tremblers and differ consistently from each other in the

TABLE 1. Sample sizes, ranges, means, and standard deviations of measurements (mm) and dimorphism indices of the subspecies of tremblers and White-breasted Thrashers.

	Males				Females				Dimorphism index[1]
	n	Min–max	$\bar{x}$	SD	*n*	Min–max	$\bar{x}$	SD	
Wing length									
C. r. pavida	25	95.2–106.8	101.26	2.89	10	95.4–102.8	98.86	2.53	2.40
C. r. tremula	15	96.0–105.1	101.49	2.68	20	92.7–102.9	97.93	2.55	3.57
C. r. ruficauda	60	87.4–101.8	95.83	2.92	28	87.6–97.6	92.64	2.75	3.39
C. g. gutturalis	10	99.2–115.5	107.76	5.59	2	97.4–110.7	104.05	9.40	3.50
C. g. macrorhyncha	30	99.4–112.6	106.20	3.42	17	96.2–109.3	102.63	3.19	3.42
C. r. tenebrosa	23	93.1–101.3	97.19	2.22	18	87.6–97.6	92.68	2.84	4.75
R. b. brachyurus	16	91.3–102.3	96.11	3.77	9	89.4–105.0	95.67	4.33	0.46
R. b. sanctaeluciae	18	98.0–111.7	106.43	4.01	10	99.5–108.5	103.38	2.80	2.91
Tail length									
C. r. pavida	21	81.2–93.8	87.79	3.57	7	82.0–88.2	85.01	2.49	3.21
C. r. tremula	13	81.8–90.6	87.36	2.67	14	79.5–89.4	85.58	2.66	2.06
C. r. ruficauda	44	71.0–84.1	79.58	2.51	17	70.3–82.6	77.22	3.05	3.01
C. g. gutturalis	8	81.1–95.6	87.79	4.80	1	83.5			
C. g. macrorhyncha	20	80.0–94.5	87.71	3.74	10	78.3–92.5	85.18	4.06	3.93
C. r. tenebrosa	15	77.4–86.5	82.15	2.46	12	72.3–83.3	78.13	3.21	5.02
R. b. brachyurus	13	69.2–83.6	76.11	4.86	9	69.0–82.7	75.60	5.05	0.67
R. b. sanctaeluciae	14	77.5–92.5	85.11	3.71	8	76.4–86.9	81.44	3.71	4.41
Tarsus length									
C. r. pavida	31	29.5–32.9	31.29	0.90	12	29.4–32.9	30.83	1.09	1.48
C. r. tremula	20	30.1–34.9	31.61	1.15	21	29.9–33.3	31.49	0.84	0.38
C. r. ruficauda	62	27.3–31.2	29.25	0.77	27	26.4–30.9	29.06	0.85	0.65
C. g. gutturalis	9	31.5–34.3	32.76	0.94	1	29.3			
C. g. macrorhyncha	32	29.3–33.5	31.28	1.05	17	29.9–33.1	31.32	0.86	−0.13
C. r. tenebrosa	23	29.3–32.2	30.84	0.65	17	28.9–31.0	29.84	0.66	3.30
R. b. brachyurus	16	29.1–32.3	30.81	1.01	10	29.6–31.7	30.52	0.67	0.88
R. b. sanctaeluciae	21	32.6–36.0	34.26	0.92	11	31.1–35.4	33.59	1.68	1.97
Culmen length									
C. r. pavida	18	32.6–38.4	35.74	1.48	7	39.4–42.8	41.23	1.12	−14.27
C. r. tremula	6	33.7–36.6	33.47	1.04	11	38.6–44.6	41.68	1.86	−16.10
C. r. ruficauda	33	30.5–34.7	32.54	1.09	13	35.7–40.6	38.63	1.45	−17.11
C. g. gutturalis	3	34.1–37.5	35.47	1.80	1	39.5			
C. g. macrorhyncha	13	38.7–43.7	40.79	1.46	8	40.8–47.6	45.18	2.16	−10.21
C. r. tenebrosa	9	33.6–35.0	34.24	0.42	9	37.6–41.0	38.88	1.09	−12.69
R. b. brachyurus	9	27.3–30.7	29.22	0.99	5	26.0–28.6	27.58	1.06	5.77
R. b. sanctaeluciae	5	30.0–33.3	31.46	1.52	2	29.5–30.0	29.75	0.35	5.59
Bill from nostril									
C. r. pavida	32	21.2–25.6	23.35	1.09	11	26.5–30.0	28.18	1.01	−18.75
C. r. tremula	16	22.0–24.9	23.18	0.82	19	25.8–31.6	28.22	1.71	−19.61
C. r. ruficauda	60	19.7–23.3	21.28	0.76	28	23.7–27.6	25.89	1.05	−19.55
C. g. gutturalis	10	21.0–24.2	22.66	0.87	2	26.7–26.8	26.75	0.07	−16.56
C. g. macrorhyncha	29	25.1–30.2	27.62	1.27	16	29.7–33.6	31.38	1.31	−12.75
C. r. tenebrosa	20	21.2–23.7	22.40	0.62	17	24.8–29.0	26.35	1.16	−16.21
R. b. brachyurus	17	16.0–19.4	17.99	0.87	10	16.2–20.6	17.83	1.22	0.89
R. b. sanctaeluciae	20	18.2–22.0	20.08	1.00	11	17.9–21.2	19.51	1.04	2.80
Wing/bill									
C. r. pavida	25	3.9–4.9	4.37	0.27	9	3.2–3.7	3.50	0.14	22.11
C. r. tremula	12	4.0–4.7	4.36	0.22	19	3.1–3.9	3.50	0.22	21.88
C. r. ruficauda	58	3.5–5.0	4.50	0.24	27	3.3–4.0	3.59	0.19	22.50
C. g. gutturalis	10	4.2–5.4	4.73	0.31	2	3.6–4.2	3.90	0.36	19.24
C. g. macrorhyncha	27	3.6–4.3	3.85	0.17	15	3.0–3.5	3.28	0.16	15.99
C. r. tenebrosa	20	4.0–4.8	4.34	0.19	17	3.1–3.8	3.51	0.18	21.15

[1] Obtained by dividing the difference between the means for the sexes by the mean for the means of the sexes and multiplying by 100.

TABLE 2. Percentage separability of tremblers from pairs of islands, based on discriminant-function analysis of lengths of wing, tarsus, and bill from nostril.

Island pair	Percentage correctly classified		Color difference
	Males	Females	
Monserrat vs. Guadeloupe	62.5[a] vs. 58.3	100[b] vs. 83.3	+
Guadeloupe vs. Dominica	100 vs. 98.2	88.9 vs. 100	+
Guadeloupe vs. St. Vincent	100 vs. 100	83.3 vs. 94.1	−
Dominica vs. St. Vincent	87.7 vs. 95.0	80.0 vs. 64.7	+
Martinique vs. St. Lucia	100 vs. 100	100[b] vs. 100	+

[a] The pairs of figures are in the same sequence as those of the islands.
[b] Sample size = 1; all others ≥ 8.

color of the underparts as described by Ridgway (1907). The color differences between the two populations of the White-breasted Thrasher (*Ramphocinclus*) are also consistent and as described by Ridgway (1907).

While the Gray Tremblers differ most markedly in color from all the Brown Tremblers, they also differ more in color between themselves than do any two populations of the Brown Trembler. Discriminant-function analysis of measurements (Table 2) indicates that they also differ more from each other than do any pair of populations of the Brown Trembler in these characters.

DISCUSSION

A potential selective advantage to sexual dimorphism and an explanation for sexual differences in bill length may be related to foraging. In his work on the Brown Trembler on Dominica, Zusi (1969) found that these birds forage in a variety of ways. They take small fruits in trees and bushes, toss leaves to uncover small animals on the ground, probe in rotting logs, take small prey from crevices on tree trunks, or probe among tangled vines, clumps of dead leaves, or epiphytes.

Zusi believed the Brown Trembler's three most important potential competitors for food on Dominica to be the Scaly-breasted Thrasher (*Margarops fuscus*), the Pearly-eyed Thrasher (*M. fuscatus*), and the Forest Thrush (*Cichlherminia lherminieri*). The bills of these species differ markedly from those of the tremblers. The bill of the Scaly-breasted Thrasher is much shorter, and those of the other two (especially the Forest Thrush) considerably heavier. Zusi (1969) found other structural adaptations related to the trembler's arboreal foraging methods. The long bill and flattened cranium are related to probing narrow spaces, and the narrow antorbital region and the eyes are "oriented for close binocular vision." The short legs are "probably an advantage for perching on vertical surfaces." His comment that the reduced sternum and wings are "possibly correlated with the reduced need for extended flight" may be true, but the straight edge of the shallow, tapered keel of the sternum resembles that of woodpeckers and woodcreepers (Dendrocolaptidae) and may be an adaptation for bringing the center of gravity of the bird nearer to the substrate to which they cling. The specific advantage of this feature cannot be determined without a more detailed study of the bird's methods of locomotion, because Zusi's (1969) figure of a trembler clinging to a tree trunk shows the bird perched horizontally on the trunk rather than vertically like a woodpecker.

Zusi was unable to determine the sex of the birds that he watched foraging, so there is no information on foraging differences related to the sexual dimorphism in bill length. Speculation on this subject may provide hypotheses to be tested in future fieldwork.

The dimorphism in bill length is presumably related to differences in its use in probing, a method of foraging not shared with the trembler's potential competitors. The longer bill of the females increases the range of depths available to them and thus the potential for an increased feeding rate. This may be important for females when extra energy is needed for the development of eggs and during incubation, when foraging time may be limited. It might also be important if the female has the larger share in feeding the young, but the relative roles of the sexes in the care of the young are not known. The latter hypothesis does not,

however, explain why the males' bills are shorter. This may be related to a possible difference in the utilization of foraging places. Perhaps the males are better adapted for working in shallow crevices or foraging on the ground and the females for probing deeply in epiphytes. A foraging study with color-marked birds on Dominica, where the birds are still numerous, should answer this question.

On Martinique and St. Lucia, tremblers are much grayer than elsewhere, are less sexually dimorphic, and are sympatric with the White-breasted Thrasher, which is only known from these two islands. Competitive interactions between the two species are possible because the bill of the White-breasted Thrasher is more similar in shape to that of the trembler than any of the other sympatric thrashers or thrushes. At present, the numbers of both species are much reduced on both islands. In spite of the limited amount of overlap today, the earlier literature indicates that both species occupied a wider range of habitats before the islands were greatly modified by European settlers, and that they were probably sympatric over large areas.

On Dominica, where the mongoose (*Herpestes*) is absent and where Brown Tremblers are not uncommon today, they occupy a fairly wide range of habitats. Zusi (1969) found them in montane forests, secondary forests, and plantations, as well as rain forests, the most usual habitat on other islands, but he did not find them in dry scrub woodland during the leafless season. According to Diamond (1973), tremblers evidently occupy "a slightly wider range of habitats on St. Lucia than on Dominica," and Danforth (1935) found Gray Tremblers "locally common chiefly in the humid virgin forest, although found to some extent in second growth and in a low, rather dry, brushy type of forest." Bond (1928) found Gray Tremblers "a considerable distance from virgin forest . . . also in the low forest which peters out into arid scrub in northern St. Lucia." Zusi (in litt.) found both species along the Rivière Sourcière, St. Lucia, where White-breasted Thrashers were in bushes or feeding on the ground whereas Gray Tremblers were in taller, leafy trees or quite low in slender, scrubby trees. At this site he only observed tremblers foraging in dried leaves caught in a tree fork.

There is less information on the White-breasted Thrasher. Diamond (1973) says that "on both islands it now occurs only on scrub forests on the windward coast, showing a distinct preference for a low woodland with thin, crowded tree trunks, no ground cover and abundant leaf litter," and adds that it "feeds chiefly on the ground and mainly by turning over leaf litter," but that "one bird was seen to pick berries off a terminal twig." He continued that it "was formerly much more widespread, at least on St. Lucia, where Semper (1872) found it common." Semper (1872) only says that he met them "busily searching amongst the bushes near the ground and in low trees." According to his field notes for Martinique, Fred A. Ober (*in* Lawrence 1878) collected White-breasted Thrashers at Trois Islets and observed one in the Jardin des Plantes at St. Pierre. He commented that it "loves deep woods and the borders of streams." Near the mouth of the Rivière Chaloupe, St. Lucia, Zusi (in litt.) found White-breasted Thrashers both in spindly, short, deciduous trees 3–6 m tall and near or on a canyon floor where the trees were 18–21 m tall and greener.

From the above evidence, it appears that Gray Tremblers once occurred in the dry scrub forest where White-breasted Thrashers occur today and that the latter once occurred in deeper forest than they do now. Within the forests, the Gray Tremblers evidently foraged higher in the trees and the White-breasted Thrashers stayed on or near the ground.

The bill of the White-breasted Thrasher is much shorter and the cranium much higher than those of the tremblers (Zusi 1969). Presumably this limits the ability of these birds to probe in epiphytes or in crevices. The keel of the sternum in the White-breasted Thrasher is deeper and rounded in outline, unlike the shallow, straight-edged keel of the tremblers (pers. obs.). Presumably, the White-breasted Thrasher is less well-adapted for clinging to tree trunks than the trembler. On the other hand, it is relatively long-legged (wing/tarsus ratio 3.1 vs. 3.4 for the tremblers), indicating that it is a more terrestrial form, which is corroborated by Bond's statement (1957) that they "are largely terrestrial." Diamond's (1973) statement that they fed by turning over leaf litter, as Zusi (1969) reported Brown Tremblers did on Dominica, suggests that the White-breasted Thrasher may have taken over this feeding niche on Martinique and St. Lucia, "forcing" the tremblers on those islands to spend more time foraging in the trees. This is supported by Zusi's observations (in litt.) of White-breasted Thrashers' clearing small areas

of leaves by grasping and tossing, or by broom-sweeping with vigorous side-to-side sweeps of the bill, or by tossing to the front.

The difference in color between the Gray and Brown tremblers is not easy to explain. Some birds, like the Fox Sparrow (*Passerella iliaca*), show color differences that appear to be associated with habitat differences (Swarth 1920). The gray color of the tremblers on Martinique and St. Lucia may have resulted from a habitat difference, but if this is so it is difficult to explain on the basis of their present distribution, because the tremblers on these islands are now largely restricted to wet forests, the habitat in which they are most numerous on other islands. However, it may not always have been thus.

If dry scrub woodland was originally more extensive on Martinique and St. Lucia than on the other islands on which tremblers occur and if tremblers were numerous in this habitat, they might have been more easily seen by aerial predators such as barn-owls (*Tyto alba*) there than in the rain forest. Thus, the advantage of a grayish plumage in scrub woodland might have outweighed its possible disadvantage in rain forest. The darker, sooty color of the White-breasted Thrashers may be related to their spending much time in shadows on or near the ground.

White-breasted Thrashers are now birds of the scrub woodlands, and sexual dimorphism in the Gray Trembler is reduced on St. Lucia. These facts suggest the possibility that the White-breasted Thrasher, which has a similarly shaped but shorter bill, may have been more in competition with males than with the longer-billed females of the Trembler. Thus sexual dimorphism in the latter may have been reduced through a greater increase in the length of the males' than the females' bills.

An alternate hypothesis is that the Gray Trembler may have arisen on one of the low-lying limestone islands east of the volcanic arc on which Brown Tremblers now occur and later may have colonized Martinique and St. Lucia. Once there, it may have replaced an existing population of the Brown Trembler. A possible source of a gray ancestral stock is Barbados, where little original habitat is left and tremblers are not known to exist. The presence of a fossil trembler on Antigua is evidence that tremblers formerly occurred on low-lying islands of the limestone arc. The finding of such a fossil on Barbados would provide support for this idea.

It is possible that, like the Gray Trembler, the White-breasted Thrasher arose on the islands of the limestone arc and were successful in colonizing only Martinique and St. Lucia, possibly because the low scrub vegetation on these islands fit the ecological conditions of the islands on which they arose and to which they were adapted.

The original source of the White-breasted Thrasher is unclear. Although its juveniles are dark-breasted like those of tremblers, Zusi (1969) believed it nearest to the Mexican and Central American genus *Melanotis*, whereas *Cinclocerthia* may be distantly related to *Margarops* (including *Allenia*), the three species forming an endemic West Indian group, whose relationships with continental mimids remain to be determined. A genetic assay of these genera, their island populations, and their mainland relatives should prove most valuable in solving these problems.

Taxonomic Conclusions

The trembler forms *gutturalis* (Martinique) and *macrorhyncha* (St. Lucia) differ markedly from trembler populations on the other islands and to a lesser extent from each other. Both have been considered separate species (Ridgway 1907). Both are brownish gray rather than reddish brown in general color, but they differ from each other in details of the color of the underparts. The birds from Martinique average slightly larger in wing and tarsus lengths than those from St. Lucia, but the latter have much longer bills and are less sexually dimorphic in this character. The differences between these two populations and the rufescent ones are comparable to or greater than those between other pairs of thrasher species (e.g. the Brown Thrasher, *Toxostoma rufum*, and the Long-billed Thrasher, *T. longirostre*). In addition, Zusi (in litt.) found differences in vocalization and in trembling between the Brown Trembler on Dominica and the Gray Trembler on St. Lucia. On Dominica the tremblers were silent while foraging, whereas on St. Lucia they gave "a loud call of repeated notes when flying to another tree (the 'song' described by Bond [1936] as like a Carolina Wren's [*Thryothorus ludovicianus*]). Trembling differs in that, on St. Lucia, it is often confined to the tail." Evidence from the tapes of Roché (1971) and Hardy et al. (1987) further indicates vocal differences between the two

tremblers. I therefore recommend that they be separated from the other tremblers as *Cinclocerthia gutturalis* (Gray Trembler) and that the English name for the remaining populations be Brown Trembler.

The birds from the other islands (*C. ruficauda*) are more similar to each other in color and are separated primarily on the basis of measurements (Table 2). Populations from Saba to Guadeloupe do not differ sufficiently in measurements from island to island to warrant separation into subspecies. On the basis of color, birds from Guadeloupe (*tremula*) were formerly separated from those from the islands to the north (*"pavida"*) by their supposedly darker color and their grayer, less tawny or ochraceous chests, but these characters do not hold up in series. In spite of their being separated geographically by the two large, grayish forms on Martinique and St. Lucia, birds of the other two reddish brown races, *ruficauda* (on Dominica) and *tenebrosa* (on St. Vincent) are more similar to each other in size than to any other form. They average smaller than *tremula* including *"pavida,"* but they differ from each other in color, *tenebrosa* being darker in overall color.

Bangs (1929) described a race of trembler as *C. r. sola*, presumably from a small island off Guadeloupe. He claimed that it differed from the Guadeloupe form in being paler like *"pavida"* but had a much longer bill. I have examined the type and only specimen referred to the new subspecies in the Museum of Comparative Zoology. Its color is similar to that of a specimen in the same collection from St. Kitts. My measurements of the type are: wing 97.4 mm, tail 84.4 mm, culmen 41.9 mm, and bill from nostril 28.3 mm. The wing/bill-from-nostril ratio is 3.4. All are well within the range of females of *pavida* and *tremula* (cf. Table 1). In his description of *"sola,"* Bangs (1929) discussed the provenance of the unique type, the only paratype of *C. r. tremula* of Guadeloupe. He found the paratype so different from a series of specimens from Guadeloupe in coloration and bill length that he named it and said that it "probably [came] from some small island near Guadeloupe, possibly Desirade." Bond (1956), without presenting reasons, "suggested" Monserrat as the type locality. In view of the sexual dimorphism and considerable individual variation in coloration, which neither Bangs nor Bond recognized, and the agreement in measurements of the type of *"sola"* with females of *tremula* (including *"pavida"*), I think it possible that this specimen actually came from Guadeloupe. In any case, there seems to be insufficient evidence to assign any type locality to *"sola."*

Ridgway (1907) considered the two forms of the White-breasted Thrasher (*Ramphocinclus*) to be distinct species. They differ considerably in size and color. The St. Lucia birds (*sanctaeluciae*) are the larger in all measurements (Table 1), and the sides and flanks of the Martinique birds (*brachyurus*) are much paler than the upperparts, not the same shade as in the St. Lucia birds. More recent authors (Hellmayr 1934, Davis and Miller 1960) have considered the two conspecific.

While it is virtually impossible to determine if the species level has been reached between bird populations on adjacent islands, I believe that the relationships among the forms of these species are best represented by the following arrangement:

Cinclocerthia ruficauda tremula (including *pavida*)
Cinclocerthia ruficauda ruficauda
Cinclocerthia ruficauda tenebrosa
Cinclocerthia gutturalis gutturalis
Cinclocerthia gutturalis macrorhyncha
Ramphocinclus brachyurus brachyurus
Ramphocinclus brachyurus sanctaeluciae

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For the loan and use of material, I am much endebted to the curators of the collections which I was permitted to examine. These collections and the number of specimens examined are listed in Appendix 2.

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APPENDIX 1. List of unsexed specimens and those assumed to have been missexed and the sex assigned to each for the purpose of analysis in this paper.

Unsexed birds assumed to be males.—*Cinclocerthia ruficauda tremula*: AMNH 504515; FMNH 29046; MCZ 66489. *C. r. ruficauda*: MCZ 115101. *C. r. tenebrosa*: ANSP 160590. *C. gutturalis gutturalis*: FMNH 29053, 29055. *C. g. macrorhyncha*: FMNH 29073, 29076.

Unsexed birds assumed to be females.—*C. r. tremula*: FMNH 29044, 29047; ANSP 108764. *C. r. ruficauda*: BM(NH) 91.7.25.6. *C. r. tenebrosa*: FMNH 29060. *C. gutturalis macrorhyncha*: AMNH 504516; FMNH 29072.

Birds sexed as females, assumed to be males.—*C. r. pavida*: BM(NH) 40.5.13.3, uncatalogued; USNM 80954. *C. r. tremula*: MCZ 76365; ANSP 628. *C. r. ruficauda*: AMNH 406603, 504507; BM(NH) 89.6.10.8; FMNH 124862; MCZ 113588, 113589; ROM 339188; UMMZ 135042; YL 25559, 25563. *C. r. tenebrosa*: BM(NH) 98.2.8.26. *C. gutturalis gutturalis*: AMNH 174754, 748590; MCZ 76311; ANSP 9068; PA 1884218. *C. g. macrorhyncha*: AMNH 174753, 39222; BM(NH) 86.8.2.192, 94.1.2.242; CM 111640; MCZ 27381, 27382, 229536; USNM 80902.

Birds sexed as males, assumed to be females.—*C. r. pavida*: AMNH 174756; BM(NH) 91.1.25.2; ANSP 86438. *C. r. ruficauda*: FMNH 124861; ANSP 81191; ROM 22734; UMMZ 134382. *C. r. tenebrosa*: BM(NH) 98.2.8.25; SW 3307, 3310. *C. gutturalis gutturalis*: BM(NH) 86.28.2.190; ANSP 9067. *C. g. macrorhyncha*: BM(NH) 86.8.2.193; MCZ 29537, 29538.

APPENDIX 2. List of specimens examined and acronyms used for collections.

Specimens examined

Cinclocerthia ruficauda pavida. Saba (14): SW 7, USNM 4, ANSP 3. St. Eustatius (1): USNM 1. St. Christopher (10): SW 1, FMNH 6, USNM 1 (type), MCZ 1, BM(NH) 1. Nevis (10): SW 8, BM(NH) 2. Monserrat (10): SW 5, AMNH 1, USNM 4. *C. r. "sola."* "Guadeloupe" 1 (type): MCZ. *C. r. tremula*. Guadeloupe (50): SW 13, AMNH 7, FMNH 6, USNM 8, MCZ 10 (including type), BM(NH) 1, ANSP 1, PA 4. *C. r. ruficauda*. Dominica (99): SW 36, AMNH 12, FMNH 4, USNM 6, MCZ 6, BM(NH) 8, ANSP 3, YL 16, UMMZ 3, ROM 4, CM 1. *C. r. gutturalis*. Martinique (17): AMNH 3, FMNH 5, USNM 1, MCZ 1 (type), BM(NH) 2, ANSP 2, PA 3. *C. r. macrorhyncha*. St. Lucia (55): SW 16, AMNH 8, FMNH 7, USNM 5, MCZ 7, BM(NH) 5, ANSP 3, PA 1 (type), UMMZ 2, CM 1. *C. r. tenebrosa*. St. Vincent (41): SW 9, AMNH 5 (including type), FMNH 5, USNM 7, MCZ 4, BM(NH) 7, ANSP 4.

Ramphocinclus brachyurus brachyurus. Martinique (39): SW 10, AMNH 5, FMNH 5, USNM 3, MCZ 4, BM(NH) 6, ANSP 4, PA 2. *R. b. sanctaeluciae*. St. Lucia (44): SW 3, ANSP 6, FMNH 6 (including type), USNM 5, BM(NH) 5, ANSP 2, YL 6, PA 1, UMMZ 4, CM 1.

Acronyms used for collections

AMNH = American Museum of Natural History, New York City; BM(NH) = British Museum (Natural History), Tring; CM = Carnegie Museum, Pittsburgh; FMNH = Field Museum of Natural History, Chicago; MCZ = Museum of Comparative Zoology, Cambridge, Massachusetts; PA = Paris Museum; ANSP = Academy of Natural Sciences of Philadelphia; ROM = Royal Ontario Museum, Toronto; SW = Collection of Albert Schwartz (now at the Museum of Zoology, Louisiana State University, Baton Rouge); UMMZ = University of Michigan Museum of Zoology, Ann Arbor; USNM = National Museum of Natural History, Washington, D.C; YL = Yale Peabody Museum, New Haven.

TERRITORY OVERLAP AND HABITAT USE OF SYMPATRIC CHICKADEES

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ABSTRACT.—We examined territorial relationships of breeding Black-capped Chickadees (*Parus atricapillus*) and Mountain Chickadees (*P. gambeli*) in the foothills of the Rocky Mountains in southwestern Alberta, where the two species are sympatric in mixed forests of river valleys. Both the minimum convex polygon method and Anderson's (1982) utilization distribution method indicated that territory size did not differ significantly between species. There was no indication of interspecific territoriality, with little intraspecific overlap of territories (0–8%) but considerable interspecific overlap (30–70%). Discriminant function analysis of habitat variables measured on randomly located plots on territories showed no interspecific differences. However, an analysis that weighted plots by relative use by birds showed a significant difference. Mountain Chickadees used areas with large conifers and dead trees more than did Black-capped Chickadees. Our results indicate that habitat preferences shown by the two species in allopatry persist in sympatry, and that local coexistence is permitted by the mosaic nature of the habitat. *Received 11 July 1988, accepted 12 December 1988.*

ALTHOUGH interspecific territoriality is believed to be common in birds (see reviews in Simmons 1951; Orians and Willson 1964; Murray 1971, 1981; Cody 1973), it remains controversial and incompletely understood. Many workers (e.g. Simmons 1951, Orians and Willson 1964, Cody 1969) have proposed that interspecific territoriality originates as an adaptive response which functions to reduce competition for resources, usually food. In contrast, Murray (1971, 1976, 1981) proposed that interspecific territoriality may arise nonadaptively as a result of misdirected intraspecific aggression. Much of the evidence (see Wittenberger 1981 and references therein) is consistent with the suggestion that interspecific territoriality has evolved as a mechanism to reduce interspecific competition, but the question of origin is far from settled.

A second controversy concerns character convergence. Cody (1969) proposed that pairs of species that are interspecifically territorial may converge in physical or behavioral characters used in territory defense (e.g. appearance or song). Character convergence is believed to enhance interspecific territoriality and further reduce competition. Murray (1976, 1981) rejected this hypothesis, arguing that it violated the competitive exclusion principle.

Many studies describing interspecific territoriality are methodologically weak (see critiques in Murray 1976, and Murray and Hardy 1981). A thorough documentation of interspecific territoriality requires demonstration that (1) territories of the species in question do not overlap, (2) non-overlap is maintained by the same behaviors used in intraspecific territoriality, and (3) non-overlap is not based on differential habitat selection (Gochfeld 1979). Few studies have fulfilled these criteria.

We investigated ecological and territorial relations of sympatric Black-capped Chickadees (*Parus atricapillus*) and Mountain Chickadees (*P. gambeli*) in southwestern Alberta. We found that though the species may compete for nest sites, they do not appear to compete for food during breeding season in this region (Hill and Lein 1988). Although never documented in North American titmice, interspecific territoriality has been suggested to occur between Black-capped and Carolina chickadees (*P. carolinensis*) and between Black-capped and Mountain chickadees (Orians and Willson 1964, but see Minock 1971). We attempted to document the occurrence of interspecific territoriality between Black-capped and Mountain chickadees, which are similar in behavior and morphology, hoping to provide evidence relevant to the resolution of questions regarding interspecific territoriality. We examined overlap in territory and habitat use by these species. Behavioral responses to natural

[1] To whom reprint requests should be sent.

and simulated territorial intrusions are dealt with in another paper (Hill and Lein MS).

STUDY AREA AND METHODS

Our study area was in the Sheep River Wildlife Sanctuary (50°38'N, 114°30'W) in the upper foothills of the Rocky Mountains, 70 km southwest of Calgary, Alberta. The two chickadee species nest in mixed forests of river valleys in this area. The forests are dominated by trembling aspen (*Populus tremuloides*), with lesser amounts of white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*), lodgepole pine (*Pinus contorta*), and limber pine (*P. flexilis*). The understory consists of young trembling aspen, willow (*Salix* spp.) and alder (*Alnus* spp.), with an undergrowth primarily of cow parsnip (*Heracleum lanatum*) and various species of grass. Anderson (1979) gives a more complete description of habitats in the study area.

TERRITORY MAPPING

Observations were made in May and June of 1983 and 1984 of color-marked male chickadees, which are more active than females in territory defense (Odum 1941). Because territory size may vary seasonally in Black-capped Chickadees (Stefanski 1967), we made observations during all stages of the breeding season (prenesting, cavity digging [Black-capped Chickadees only], nest building, laying, incubating, and nestling stages). Few pairs were located during the prenesting stage, and thus observations on most pairs began during the cavity-digging stage (for Black-capped Chickadees, which excavate their own cavities) or the nest-building stage (for Mountain Chickadees, which are secondary cavity nesters). At least once during each breeding stage, each focal male was followed by two observers who recorded its location at 5-min intervals. An interval of this length (during which a chickadee could easily travel to any point within its territory) reduces autocorrelation of location data, which may bias many territory-mapping methods (Swihart and Slade 1985). Locations were plotted on a 1:5680 aerial photograph. Fine details, including individual conifers, could be discerned, permitting accurate plotting (estimated accuracy to within 2 m). Map locations were subsequently converted to Cartesian (x, y) coordinates by digitizing them on a Calcomp 9000 tablet.

All observations were made between 0500 and 1300 (MDT). We followed focal birds until 30 locations were recorded. On occasions when a bird was lost from view, observations continued after the bird was relocated. Occasionally, fewer than 30 locations were recorded. Observations of individual birds usually lasted ca. 2.5 h, but were occasionally as long as 4 h. We believe that a period of 2.5–4 h is sufficient for a chickadee to travel to most areas within its territory. Odum and Kuenzler (1955) found that 2–8 h of observation were necessary to plot the territories of several species adequately. Stefanski (1967) used an observation period of only 1 h (but repeated approximately 3 times per stage of the breeding cycle) in plotting Black-capped Chickadee territories.

Because the best method for mapping territories is controversial (reviews in Van Winkle 1975, Ford and Myers 1981, Anderson 1982), we used both the conventional minimum convex polygon (MCP) method and the utilization distribution (UD) method of Anderson (1982) to map territories and calculate territorial overlap. We assume that territory is equivalent to home range in these chickadees. Field observations suggest that this assumption is reasonable; 18 of 20 incidents of territorial defense (either strong countersinging or chases) were at or very near an outermost location. Thus both species appeared to defend the entire area that they utilized.

Minimum convex polygon (MCP) method.—We calculated areas of MCPs containing locations for each territorial male during each stage of the breeding cycle, and also for each male with locations pooled from all breeding stages. Observation-area curves were calculated for each male to ascertain that sample sizes were adequate. Territory boundaries were determined by connecting the outermost locations for each male on a map of the study area. Areas of each territory and of each region of intra- and interspecific overlap were calculated using a Calcomp 9000 digitizing tablet.

Utilization distribution (UD) method.—Anderson's (1982) program uses a set of locations to produce a UD for each individual. The UD is a large, two-dimensional matrix, whose values represent the probability of occurrence of an individual at a specific pair of coordinates. UDs may be converted to contour maps using a suitable graphics program. Each contour connects loci with the same probability of an individual being present.

This method assumes that observations are independent. We took two precautions to guard against autocorrelation. First, as mentioned previously, observations were made at intervals which were relatively long compared to the time required for a bird to cross its territory. Second, we used relatively large sample sizes. The utilization distribution method is moderately insensitive to sample-size bias if data are independent. However, autocorrelation problems are most serious when sample sizes are small (Schroder 1979, Anderson 1982). Braun (1985) felt that 50 observations were a sufficiently large sample to avoid problems of autocorrelation. Therefore, we used data pooled from all stages of the breeding cycle.

Observations of Black-capped Chickadees engaged in digging nest cavities were excluded from the analysis. Several males showed concentrations of locations around the nest site during this stage. This concentration influenced the shape of the UD. Mountain Chickadees do not dig cavities and thus would not

have this concentration of observations surrounding the cavity. This eliminated 10.5% of Black-capped Chickadee locations in 1983 and 2.9% in 1984.

Contour maps of UDs were made with the SURFACE II graphics package. To assess territory overlap it was necessary to choose a contour to represent the territory boundary. Choice of a contour of too high a probability excludes many observations and thus reflects actual territory boundaries poorly. Choice of contours of extremely low probability results in very large areas (Anderson 1982) and may include regions where no observations were made. We examined the position of several contours and chose the $P = 0.0005$ contour, which enclosed most of the observations, and all of the observations of territory defense, as the territory boundary. The area within this contour may be of any shape; it need not be a convex polygon and may consist of two or more disjunct portions. We overlaid transparent copies of contour maps on the original mosaic map and calculated territory areas for each individual, and the areas of intra- and interspecific overlap, with the Calcomp 9000 digitizing tablet.

Habitat Analysis

We randomly chose five circular plots (11.0 m in diameter, area of ca. 0.01 ha) per territory, and measured habitat variables using a modification of the method of James and Shugart (1970) and James (1971). Because observer bias can affect data collected using this technique (Gotfryd and Hansell 1985), Hill made all measurements.

Birds are believed to select their habitat using the overall configuration of vegetation structure (the "niche-gestalt") and not details of microhabitat (James 1971). Consequently, we measured only major structural features. All trees (vegetation with a diameter of main stem at breast height [DBH] of ≥ 8.0 cm) within each plot were categorized by species, size class (in 8.0 cm increments), and condition (living or dead). Estimates of canopy cover and ground cover were made along two transects of the plot which intersected at a 90° angle. Ten readings (five per transect) for the presence or absence of green vegetation were made by sighting directly up or down through a tube of 3.0 cm diameter held at arm's length. We used the proportion of readings with vegetation present to estimate cover. Shrub density was estimated by counting the number of stems <8.0 cm DBH intersected along two 2-m-wide transects (area of ca. 0.005 ha) made across the plot. Average canopy height was measured using a clinometer.

We initially recorded 33 variables. Because most plots contained only one or two tree species, each of relatively uniform size, many cells in the data matrix were empty. Therefore, we used combined categories of small deciduous, large deciduous, small coniferous, and large coniferous trees for analysis. Because the five plots on each territory cannot be considered as independent samples, we used mean values for each territory in statistical analyses. We also calculated four additional variables (proportion of plots per territory with 0, 1, 2, or 3 tree species, respectively), which give an indication of tree species diversity within each territory. A full description of variables used in analyses is given in the Appendix.

All variables measured as percentages or proportions were arcsine transformed for analysis. Two-sample *t*-tests evaluated differences in habitat variables between territories of the two species. Subsequently, we performed discriminant function analysis (DFA) with the DISCRIMINANT procedure of SPSS (Hull and Nie 1981). The first analysis (the habitat DFA) determined whether the habitats differed consistently between territories of the two species. This analysis used mean values for the five plots on each territory, with 14 Black-capped Chickadee and 8 Mountain Chickadee cases analyzed.

Because each territory contained patches of different habitat types, it is possible that species with different habitat requirements could fulfill these requirements in territories with similar overall habitats through differential use of the habitat mosaic. Clearly, the habitat DFA would test only for differences in the available habitat, but would not reflect differences in the utilized habitat. Therefore, we developed a procedure to weight each plot according to the relative amount of time that the resident spent in that portion of the territory. We assigned each plot a relative weighting of 1 (least use) through 5 (greatest use). Weightings for each plot were determined from the UDs. The plot falling within the contour with the highest probability of use was assigned a weight of 5, the plot falling within the next highest contour was assigned a weight of 4, etc. When two plots occurred on or between the same contours, both were assigned the mean weighting. For example, if two plots occurred within the highest probability region each would receive a weight of 4.5; i.e. $(5 + 4)/2$. Weightings summed to 15 for each territory.

A utilized habitat DFA was subsequently run using the weighted data. SPSS permits the weighting of cases, treating the importance of each case in a way directly proportional to the weighting. In using this technique we abandoned the one territory/one observation case protocol used in the habitat DFA and thus violated the assumption that each data point is independent. We recognize this violation and consider this aspect of the analysis as exploratory rather than confirmatory.

In both DFAs the equality of group variance-covariance matrices were evaluated using Box's *M* (Pimentel 1979). Neither DFA showed a significant difference between group variance-covariance matrices. Because the smallest group in the habitat DFA consisted of 8 cases (territories), only 7 variables could be used in this analysis. Although the number of samples in the utilized habitat DFA was larger (40 in

the smallest group), the data also came from 8 territories, and we therefore limited this analysis to 7 variables as well. We used stepwise analyses to determine the first 7 variables to enter each analysis. Variables are selected for entry on the basis of their discriminatory power (Klecka 1975). However, because the order of entry in a stepwise DFA can be determined by trivial sample differences that do not reflect population differences (Tabachnick and Fidell 1983), we did not accept that the order of entry of the variables necessarily reflected their power to discriminate. Therefore, we also ran direct DFAs with various different combinations of variables to look for the optimal combination of 7 variables (as judged by the loadings of the variables and the ability to correctly classify the data). Both stepwise and direct methods revealed the same 7 variables with the greatest discriminatory power.

The DISCRIMINANT procedure of SPSS allows for adjustment of the probability of group membership for classification purposes. Normally, an adjustment is made when there is prior knowledge of a skewed population distribution between groups. Often the relative sample sizes of the groups is used to assess whether population distributions are skewed. Because our sample distribution of cases suggested the possibility of population differences between species, we ran analyses with both equal and adjusted prior probabilities. The actual success of the DFAs was evaluated using F tests of the significance of the Mahalanobis distance between groups (a test for the equality of multivariate means) and Cohen's Kappa, a statistic which evaluates the improvement of the classification of the discriminant function over chance alone (Titus et al. 1984).

RESULTS

Territory areas and overlap.—We collected data from 8 territorial males (5 Black-capped Chickadees and 3 Mountain Chickadees) in 1983 and 14 males (9 Black-capped Chickadees and 5 Mountain Chickadees) in 1984. These included all territorial chickadees in the study area. In 1983 we obtained a mean of 136.8 locations per Black-capped Chickadee territory (mean of 27.4 locations per breeding stage) and a mean of 109.6 locations per Mountain Chickadee territory (mean of 27.4 locations per stage). No territory was represented by fewer than 100 observations. In 1984 the average number of locations per territory dropped slightly, with a mean of 115.4 locations for Black-capped Chickadee territories (23.1 per stage) and a mean of 99.8 locations for Mountain Chickadee territories (25.0 per stage). In 1984 one Black-capped Chickadee territory (with 92 locations) and three Mountain Chickadee territories (with 68, 89, and 90 locations) were represented by less than 100 observations.

We found no consistent relationship between territory area and stage of breeding cycle for either species. Only 3 of 14 Black-capped Chickadee territories, and 4 of 8 Mountain Chickadee territories, decreased in area as the breeding season progressed, a pattern reported by Stefanski (1967) for Black-capped Chickadees. The other territories showed no consistent pattern of seasonal variation in area. Therefore, we combined data from all stages of the breeding cycle. All observation-area curves exhibited asymptotes, indicating that sample sizes were sufficiently large for accurate estimation of territory size (Odum and Kuenzler 1955).

Both the MCP method and the UD method (using the $P = 0.0005$ contour) produced similar mean territory areas (Table 1). Mean estimated territory sizes did not differ between techniques for either species, nor were there significant differences between species or between years (t-tests, all $P > 0.25$).

None of the territories exhibited intraspecific overlap in 1983, as mapped using the MCP method (Fig. 1A). In contrast, all three Mountain Chickadee territories overlapped Black-capped Chickadee territories. Mean interspecific overlap (including only those territories with interspecific overlap) was 33.0% for Black-capped Chickadees and 40.0% for Mountain Chickadees (Table 2).

The same pattern of little intraspecific overlap and large interspecific overlap was also seen in 1984, although five of nine Black-capped Chickadee territories showed some intraspecific overlap (mean of 6.8%) when the MCP method was used (Table 2, Fig. 2A). Every Mountain Chickadee territory, however, was overlapped by at least one Black-capped Chickadee territory (Fig. 2A), with mean interspecific overlap of 32.8% for Black-capped Chickadees and 69.4% for Mountain Chickadees (Table 2). The larger value for Mountain Chickadees reflects the fact that in three cases a single territory overlapped more than one Black-capped Chickadee territory, with only a small portion of each Mountain Chickadee territory not overlapping.

The utilization distribution method produced similar results (Figs. 1B, 2B). In 1983 only two small regions of intraspecific overlap (both involving Black-capped Chickadees) were found (Fig. 1B), with a mean overlap of only 2.7% (Ta-

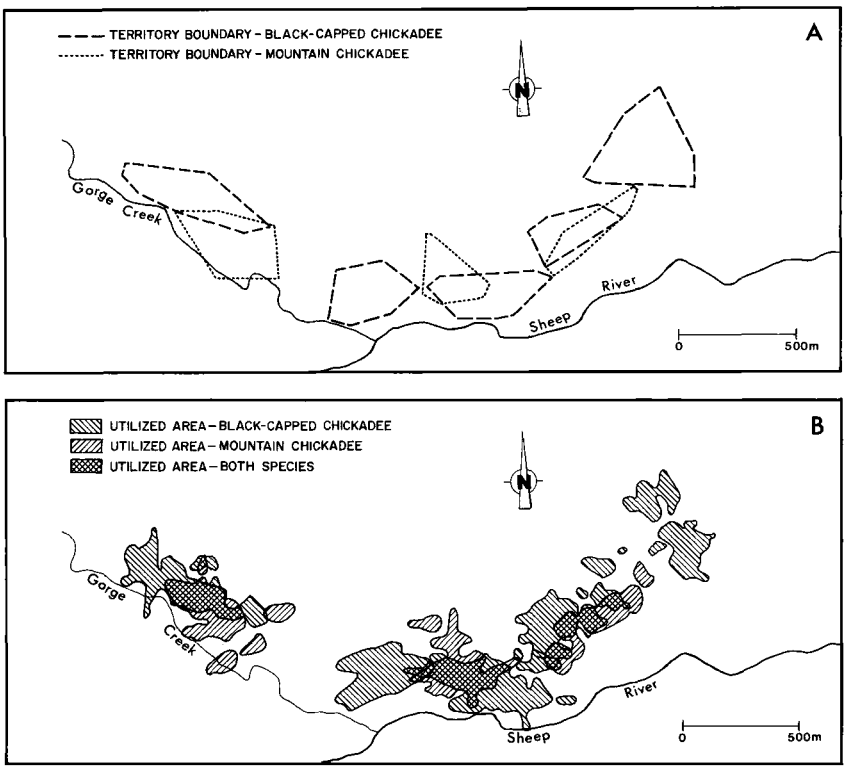

Fig. 1. Territory boundaries of Black-capped Chickadees and Mountain Chickadees in 1983. (A) As determined by the minimum convex polygon method. (B) As determined by Anderson's utilization distribution method.

ble 2). In contrast, every Mountain Chickadee territory overlapped at least one Black-capped Chickadee territory, with mean interspecific overlap of 28.4% and 46.1%, for Black-capped and Mountain chickadees, respectively (Table 2).

Increased intraspecific overlap during 1984 was also found using the UD method. However, although the number of regions of intraspecific overlap increased (from 2 to 6 for Black-capped Chickadees and from 0 to 2 in Mountain Chickadees), the area overlapped was small (Fig. 2B), with mean intraspecific overlap of 8.1% for Black-capped Chickadees and 4.9% for Mountain Chickadees. As in 1983, there was extensive interspecific overlap, with mean overlap values of 35.7% and 52.4%, for Black-capped and Mountain chickadees, respectively (Table 2).

TABLE 1. Areas (ha) of territories of Black-capped Chickadees and Mountain Chickadees calculated by the minimum convex polygon (MCP) and Anderson's utilization distribution (UD) methods. Values are $\bar{x} \pm$ SD.

	Territory area (ha)					
	1983		1984		Both years combined	
Method	Black-capped Chickadee ($n = 5$)	Mountain Chickadee ($n = 3$)	Black-capped Chickadee ($n = 9$)	Mountain Chickadee ($n = 5$)	Black-capped Chickadee ($n = 14$)	Mountain Chickadee ($n = 8$)
MCP	9.47 ± 2.48	6.95 ± 3.14	8.43 ± 4.47	6.18 ± 4.03	8.80 ± 3.80	6.47 ± 3.50
UD	7.91 ± 0.95	6.88 ± 1.03	7.76 ± 2.57	7.34 ± 1.92	7.81 ± 2.08	7.18 ± 1.57

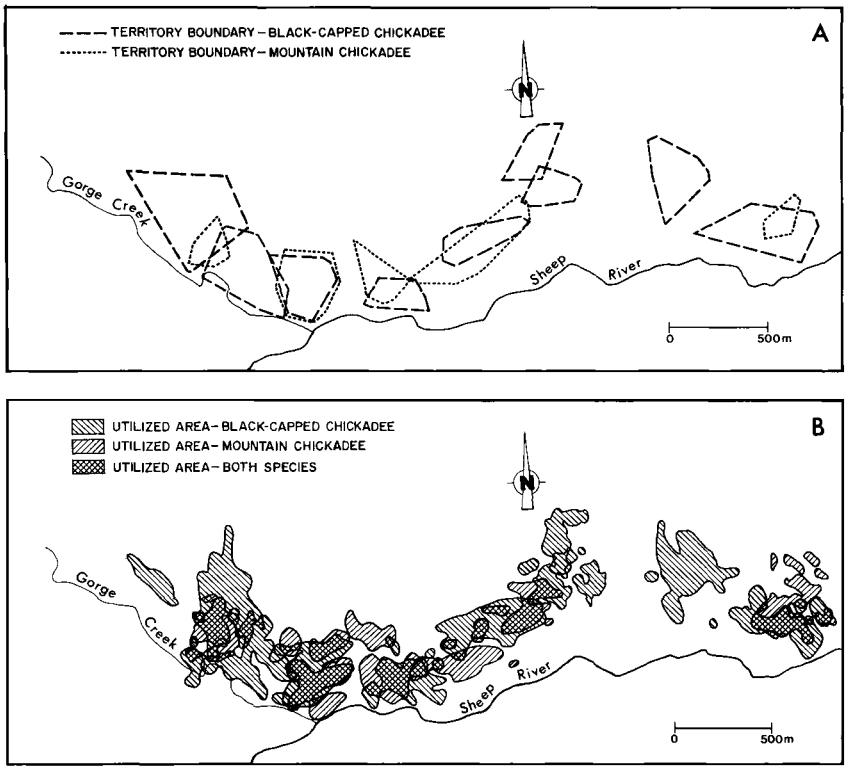

Fig. 2. Territory boundaries of Black-capped Chickadees and Mountain Chickadees in 1984. (A) As determined by the minimum convex polygon method. (B) As determined by Anderson's utilization distribution method.

Habitat analysis.—In total, we sampled 110 plots on 22 territories (14 Black-capped Chickadees and 8 Mountain Chickadees) over two summers. None of the measured habitat variables differed significantly between territories of Black-capped Chickadees and Mountain Chickadees (Table 3). In the habitat DFA, the function providing greatest separation was not significant ($P = 0.64$). In addition, the overall correct classification rate of the original data set using either equal or adjusted prior probabilities of group membership was only 63.6%, which is not significantly better than chance (Kappa = 0.214, $P > 0.18$).

The utilized habitat DFA produced a function with significant separation of territories of the

TABLE 2. Overlap between territories of Black-capped Chickadees and Mountain Chickadees, calculated from minimum convex polygon (MCP) and Anderson's utilization distribution (UD) methods. Percentage overlap was defined as total area of overlap on a specific territory divided by the total area of the overlapped territory × 100. Mean values were calculated using only territories that exhibited overlap. Values are $\bar{x} \pm$ SD (n).

		Percentage overlap			
		Intraspecific overlap		Interspecific overlap	
Year	Method	Black-capped Chickadee	Mountain Chickadee	Black-capped Chickadee	Mountain Chickadee
1983	MCP	— (0)	— (0)	33.0 ± 16.3 (3)	40.0 ± 20.7 (3)
	UD	2.7 ± 1.0 (2)	— (0)	28.4 ± 15.9 (4)	46.1 ± 8.2 (3)
1984	MCP	6.8 ± 2.6 (5)	— (0)	32.8 ± 31.6 (7)	69.4 ± 25.7 (5)
	UD	8.1 ± 6.6 (6)	4.9 ± 0.8 (2)	35.7 ± 24.1 (7)	52.4 ± 10.2 (5)

TABLE 3. Habitat variables measured in territories of Black-capped Chickadees and Mountain Chickadees. See Appendix for explanations of acronyms for variables.

Variable[a]	Black-capped Chickadee ($n = 14$)	Mountain Chickadee ($n = 8$)	P[b]
SMADEC	12.46 ± 8.10[c]	13.92 ± 7.47	0.68
LARDEC	1.91 ± 1.70	2.22 ± 1.90	0.70
SMACON	3.53 ± 5.50	4.65 ± 6.88	0.68
LARCON	0.80 ± 1.50	1.60 ± 3.20	0.43
TOTTREE	19.20 ± 9.67	22.33 ± 9.77	0.48
NUMDEAD	1.91 ± 1.11	2.09 ± 1.14	0.73
PERCDEAD (%)	14.61 ± 3.53	15.04 ± 4.08	0.83
CANHT (m)	12.61 ± 4.07	13.13 ± 3.37	0.76
CANCOV (%)	35.31 ± 6.87	36.98 ± 10.47	0.65
GRCOV (%)	51.83 ± 9.13	52.83 ± 13.66	0.84
SHRUB	17.67 ± 9.85	12.58 ± 4.84	0.19
PROP0 (%)	29.03 ± 14.44	20.93 ± 23.61	0.33
PROP1 (%)	37.01 ± 16.88	37.38 ± 10.13	0.96
PROP2 (%)	24.50 ± 14.40	27.88 ± 14.34	0.60
PROP3 (%)	15.10 ± 16.22	14.58 ± 21.13	0.95

[a] Units are counts, unless given in parentheses.
[b] Two-tailed, two-sample t-test.
[c] Mean ± SD.

two species ($P = 0.004$). The highest correct classification rate of the original data set (65.9%) was obtained using prior probabilities adjusted to the proportion in the sample, and was very close to being a significant improvement over chance (Kappa = 0.109, $P < 0.06$). The variables with greatest discriminatory power were NUMDEAD, LARCON, and SHRUB (Table 4). Mountain Chickadees used plots with more dead trees (Mountain Chickadee weighted mean of 2.00 vs. Black-capped Chickadee weighted mean of 1.28), more large conifers (1.73 vs. 0.72), and fewer shrubs (1.40 vs. 1.92) than did Black-capped Chickadees.

DISCUSSION

The similarity of territory sizes between years for either species and between species for either year is not surprising. The area that an animal uses may be affected by several factors, including food abundance and distribution, competitor density, predator density, and body-size (see reviews in Brown 1964, Schoener 1968, Davies 1978, Morse 1980, Davies and Houston 1984). We have no reason to believe that any of these factors changed significantly between breeding seasons. In addition, conditions that might indirectly affect territory size (e.g. extreme climatic differences influencing food abundance) did not vary noticeably between years. The number of chickadee territories in the study area increased from 8 in 1983 to 14 in 1984. While we cannot explain this increase in population size, we do not believe that it influenced territory size because the habitat was clearly not saturated in 1983 (most "new" territories in 1984 were in regions that were unoccupied in 1983; see Figs. 1A, 2A) and thus the increase was accommodated without a significant reduction in territory size (Table 1).

TABLE 4. Correlations between the discriminant function and the optimal group of discriminating habitat variables for the utilized habitat DFA. See Appendix for explanations of acronyms for variables.

Variable	Correlation
NUMDEAD	0.622
LARCON	0.595
SHRUB	−0.561
TOTTREE	0.465
NUMTRSP	0.413
LARDEC	0.400
CANCOV	0.355

Both the MCP and UD techniques indicated greater interspecific than intraspecific overlap for both species. Thus, if any interspecific spacing mechanism is operating, it does not result in complete interspecific exclusion. However, interspecific territoriality is not necessarily an all-or-none phenomenon. Several authors (e.g. Ebersole 1977, Mahoney 1981) indicated that the level of aggression between species, and the degree of interspecific territoriality exhibited, may vary directly with the extent of resource

competition between them. Kohda (1984) found that an individual may defend different types of territories (of different size) against different species of competitors. We found that individual Black-capped and Mountain chickadees do not exclude each other from their territories. They may differentially defend regions of their territory which contain resources of particular value. These species probably do not compete for food but may compete for nest sites (Hill and Lein 1988). The best strategy may be to ignore heterospecifics throughout most of the territory, except in the region of the nest. Such partial interspecific territoriality would not be revealed by an examination of overlap of entire territories.

No differences in habitat were found between breeding territories of Black-capped and Mountain chickadees. While this finding is based on small sample sizes and should be interpreted with caution, there are several reasons for accepting it. First, because the classification in the habitat DFA was performed on the original data set, there was likely an upward bias in the correct classification rate (Morrison 1969). Even with this bias, the classification rate was not better than that expected by chance. Thus, the conclusion of no difference between habitats of the two species based on the classification rate is conservative.

Second, because of the high degree of interspecific territorial overlap, much of the occupied habitat is the same. Every Mountain Chickadee territory overlapped at least one Black-capped Chickadee territory (see Figs. 1, 2), and some were almost totally contained within Black-capped Chickadee territories. A lack of demonstrable interspecific differences in habitat is therefore not surprising.

However, the utilized habitat DFA suggested that these species use habitat differently. These results should be considered preliminary for several reasons. First, as mentioned previously, the data violated the assumption of independence. Second, although more cases were used in this analysis, the effective sample size was no larger than in the habitat DFA and thus was small. Third, the classification rate, which verged on a significant improvement over chance, was also subject to the upward bias associated with reclassification of original data sets.

Finally, our weighting technique could be subject to criticism. We used a relative weighting scale that allowed each territory to have an equal overall effect on the analysis. However, this may have exaggerated or diminished the difference in absolute use between plots. For example, if a plot assigned the lowest weighting (1) within the territory was on the $P = 0.0005$ contour and the plot assigned the highest weighting (5) was on the $P = 0.005$ contour, then a tenfold difference in actual use would be reduced to a fivefold difference in weightings. Also, this technique relies heavily on the accuracy of the contour placement on the UDs. The program generating these contours "smooths" the data, resulting in an unknown degree of error in placement of contours.

Many authors (e.g. Dixon 1961, Minock 1971) have noted that Black-capped Chickadees normally occur in deciduous forest and Mountain Chickadees in coniferous forest. Our results indicate that even when these species occur sympatrically, Mountain Chickadees tend to use parts of the habitat mosaic with conifers (especially large conifers) more than do Black-capped Chickadees. The habitat preferences exhibited by these chickadees in allopatry seem to persist when they are in sympatry. The greater occurrence of dead trees in areas used by Mountain Chickadees may reflect their preference for dead trees (or an avoidance by Black-capped Chickadees). Alternatively, this difference may merely reflect a correlation between the presence of large conifers and dead trees. Because neither species of chickadee commonly forages in shrubs (Hill and Lein 1988), the difference in abundance of shrubs in areas used by the two chickadee species probably reflects a positive correlation of shrub abundance with the abundance of deciduous trees.

Because the observations used to produce the UDs were dominated by foraging behavior (80–85% of the observations were of foraging birds), the variables contributing most heavily to the discriminant function should relate to differences in foraging. Thus, based on the differences in utilized habitat, we should expect to find interspecific differences in foraging behavior, with Mountain Chickadees foraging more extensively in large conifers or dead trees than do Black-capped Chickadees. Such differences occur (Hill and Lein 1988).

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APPENDIX. Description of variables used in the habitat analysis.

Code	Description of variable
SMADEC	Mean number of small deciduous trees (DBH of 8.1–24.0 cm) per plot.
LARDEC	Mean number of large deciduous trees (DBH > 24.0 cm) per plot.
SMACON	Mean number of small coniferous trees (DBH of 8.1–24.0 cm) per plot.
LARCON	Mean number of large coniferous trees (DBH > 24.0 cm) per plot.
TOTTREE	Mean total number of trees per plot.
NUMDEAD	Mean number of dead trees per plot.
PERCDEAD	Mean percentage of trees that were dead per plot.
CANHT	Mean canopy height per plot, measured to nearest 0.5 m.
CANCOV	Mean percentage canopy cover for all plots within a territory.
GRCOV	Mean percentage ground over for all plots within a territory.
SHRUB	Mean number of shrubs along two 2-m-wide transects per plot.
PROP0	Proportion of plots per territory with 0 tree species.
PROP1	Proportion of plots per territory with 1 tree species.
PROP2	Proportion of plots per territory with 2 tree species.
PROP3	Proportion of plots per territory with 3 tree species.

DETERMINATION OF CLUTCH SIZE IN THE LEAST FLYCATCHER

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ABSTRACT.—We examined three factors (predation rate, incubation ability, and feeding ability) that might limit clutch size in the Least Flycatcher (*Empidonax minimus*) in an area where large emergences of midges (Chironomidae) provided abundant food for adults and nestlings. Clutch size ranged from two to five eggs, but clutches of four were most frequent (78.6% of 192 clutches) during our study. Rate of nest predation was not correlated with either clutch or brood size which suggests that Least Flycatchers did not lay smaller clutches in order to minimize predation. Incubation efficiency declined as clutch size increased, but both natural and experimental clutches of five produced more hatchlings than clutches of four. Brood size was not limited by incubation ability of females. Least Flycatchers successfully raised broods larger than the modal clutch size; neither growth rates (as measured by mass and tarsus length) nor relative survival after fledging (as indicated by frequency of recapture in mist nets) varied with brood size. We suggest several alternative hypotheses to explain why larger clutches were not more common in this local area of food abundance. *Received 18 February 1988, accepted 14 December 1988.*

LACK (1954) proposed that clutch size in altricial birds is determined by the maximum number of young that parents can feed adequately. One testable prediction of this hypothesis is that modal clutch size also should be the most productive. Nonetheless, brood enlargement experiments designed to test the "food-limitation" hypothesis have been equivocal (see summary in Lessells 1986). In some species, broods with extra young fared worse than young in normal-sized clutches (e.g. Mourning Dove, *Zenaida macroura*, Westmoreland and Best 1987), while in others, enlarged broods produced more surviving young (e.g. Blue Tit, *Parus caeruleus*, Nur 1984a). Although enlarged broods sometimes were more productive, young from these nests often fledged at below average mass (e.g. European Starling, *Sturnus vulgaris*, Crossner 1977). Because postfledging survival is correlated positively with prefledging mass (Perrins 1965), an increase in the number of fledglings does not in itself disprove the food-limitation hypothesis. Only when brood-enlargement experiments produce more surviving offspring can this hypothesis be rejected (Lack 1954).

The ability to provide food for a growing brood is probably the most fundamental factor governing clutch size in altricial birds. However, several alternative hypotheses have been proposed to explain why some birds seem capable of raising enlarged broods (see review in Murphy and Haukioja 1986). By manipulating clutches and broods, we tested three factors that might constrain clutch size in Least Flycatchers (*Empidonax minimus*).

First, we recorded the risk of predation in relation to clutch size, because selection might favor reduced clutches if predation falls disproportionately upon large clutches (Skutch 1949). Large clutches could experience higher predation rates for various reasons (see review in Slagsvold 1982a). For example, laying larger clutches necessitates a longer nesting cycle and, as a result, increases the duration of exposure to predators. Larger broods also might attract more predators if they require larger and more conspicuous nests (Snow 1978) or if parents must increase the number of trips to and from the nest (Skutch 1949).

Second, we increased clutch size to determine if brood size was limited by the inability of females to incubate a larger number of eggs. Although most birds are able to hatch more chicks in experimentally enlarged clutches (e.g. American Coot, *Fulica americana*, Fredrickson 1969; Fieldfare, *Turdus pilaris*, Slagsvold 1982b), some apparently cannot (e.g. Long-tailed Skuas, *Stercorarius longicaudus*, Andersson 1976; various Charadrii, Hills 1980). In the latter species, the number of eggs laid by a female corresponds to the maximum she can successfully incubate or brood; the upper limit is below that which could be raised (Lack 1947, Cody 1966).

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Finally, we increased brood size to determine whether clutch size was limited by the brood-rearing ability of adult Least Flycatchers. Because feeding demands of fledglings may exceed those of nestlings (e.g. Morehouse and Brewer 1968), we used both growth rates of nestlings and their relative survival to independence as measures of brood-rearing success.

METHODS

Study area.—The Least Flycatcher is a small, insectivorous passerine that nests at high densities in the dune-ridge forest at Delta Marsh, Manitoba (see MacKenzie 1982). This area is characterized by large, periodic emergences of adult midges (Chironomidae; see Fig. 1) which form the major component of both adult (Pohajdak 1988) and nestling diets (Briskie 1985). Clutches are initiated in late May and early June and in most years coincide with the first large emergences of midges (unpubl. data). A detailed description of breeding chronology and migration in this population is given by Sealy and Biermann (1983).

Flycatchers built compact, open-cup nests in crotches or saddled on limbs of deciduous trees at heights ranging from 1.0 to 11.7 m ($\bar{x} \pm$ SE: 4.1 $\pm$ 0.2 m, n = 100). Nests were located by searching suitable breeding habitat within a 3-km length of the dune-ridge forest. We monitored 348 active nests (i.e. containing at least one egg) from 1984 to 1986. In 1987, we used 19 additional nests in clutch-size manipulations.

Seasonal change in arthropod abundance was determined by taking three sweep-net samples once every 5 days from clutch initiation (late May) until the end of the breeding season (mid-August). Each sample consisted of 40 non-overlapping sweeps through the vegetation with a 37-cm diameter net at heights of 0.5 to 4.0 m. Counts from the three samples were averaged to estimate arthropod abundance on that day. All estimates were normalized by log transformation.

Nest success.—Upon discovery, each nest was flagged with numbered tape and visited every 1–3 days to monitor progress. As some nests were located after clutch initiation, we calculated nesting success using the Mayfield (1975) method. To test the nest-predation hypothesis, we compared differences in daily survival probabilities among clutch sizes (Hensler and Nichols 1981). Differences were deemed significant at a level of $P < 0.10$ because this test is prone to Type II error (Hensler and Nichols 1981). Separate survival estimates were calculated for egg laying, incubation, and nestling periods. The *incubation period* was defined as the time from laying of the final egg to hatching of the first nestling. The *nestling period* was the time from hatching of the first nestling to fledging of the last nestling. These are not standard definitions of nestling and incubation periods but represent instead the periods with or without nestlings, respectively. We felt this division was more appropriate because it reflects two periods of very different levels of parental activity.

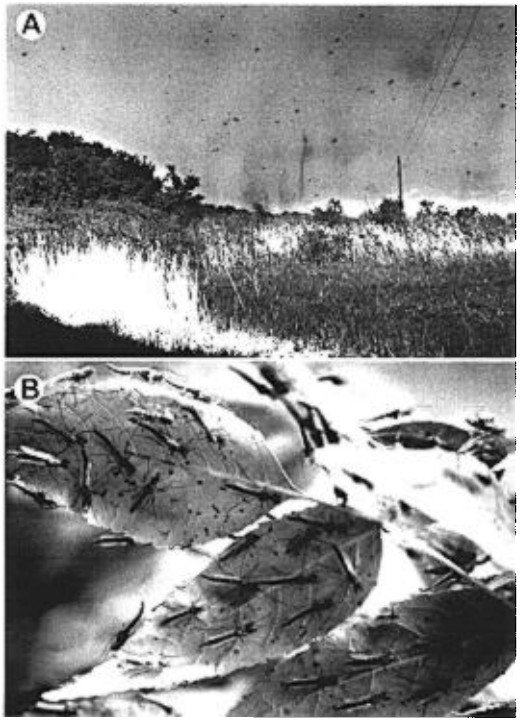

Fig. 1. (A) Adult chironomids swarming along the southern edge of the dune-ridge forest, Delta Marsh, Manitoba, June 1986. (B) Adult chironomids on foliage of dune-ridge forest.

Clutch size.—To avoid including clutches reduced by partial nest predation or egg loss, we recorded clutch size only in nests visited during laying or within the first 5 days after clutch completion. Although clutch size still might be underestimated by loss of one or more eggs during laying or early incubation, observations of egg losses in nests monitored closely during this period indicated this error was small. We visited 106 nests daily during laying and only 5 (4.7%) experienced partial clutch loss, compared to 26 (24.8%) clutches which were completely removed.

We excluded nests parasitized by Brown-headed Cowbirds (*Molothrus ater*) from the analysis because cowbirds sometimes remove host eggs (Friedmann 1963). Least Flycatchers accept cowbird eggs (Briskie and Sealy 1987a); thus, all other clutches probably were not altered through unobserved parasitism.

Hatching success and incubation ability.—Under the incubation-ability hypothesis, the modal clutch size of four eggs (see later) should produce the greatest number of hatchlings. To examine this possibility, we

recorded hatching success in natural clutches of three, four and five eggs. In 1987, we tested the ability of Least Flycatchers to incubate five eggs by adding one or two eggs to 19 nests during laying or early incubation. Hatching success was defined as number of young that hatched relative to number of eggs present just before hatching began.

Growth and survival in relation to brood size.—We measured growth and survival of nestlings to determine if modal brood size was most productive. Upon hatching, all nestlings in a random sample of each brood size were marked individually with nontoxic felt ink. The day the first nestling hatched was defined as Day 0. Beginning at Day 2, all nestlings were measured every 48 h (±1 h) to 10 days post-hatching (mean nestling period: 14.9 ± 0.2 days, $n = 36$). Hatching was asynchronous, and the day nestlings were measured corresponds only to the age of the first-hatched young. Because length of hatching spread increased with clutch size (Briskie and Sealy 1989), larger broods contained younger last-hatched nestlings than smaller broods. Taking an average of all young in a brood would have spuriously depressed mean nestling size in larger clutches, so we compared growth rates between broods by using the mean of only the three oldest nestlings within each brood. Hatching sequence did not affect growth rates within a brood size (Briskie and Sealy 1989), so we felt justified in restricting our analysis in this manner.

We used mass and tarsus length to estimate growth rate. Nestling mass was recorded to the nearest 0.1 g with a triple beam balance from 24 to 30 June 1984, and with an Ohaus digital scale for the remainder of 1984 and all of 1985. Young were not weighed in 1986 or 1987. Nestlings were induced to defecate by handling before being weighed. Tarsus length was measured to the nearest 0.1 mm with sliding calipers. Each nestling was banded with a numbered aluminum band and a year-specific color band. There were no differences in growth rates between 1984 and 1985, so data were combined in further analyses.

In 1985, seven broods of five nestlings were created by transferring a single nestling within 4 h after it hatched. Young were added to broods of four such that normal hatching asynchrony was maintained as closely as possible. Transferred nestlings came from a variety of hatching sequences but all were placed into foster nests as "last-hatched" nestlings. All were accepted by their foster parents.

To compare the growth of nestlings in relation to brood size we fitted growth curves to the logistic equation,

$$M(t) = A \cdot (1 + \exp[-K\,(t - I)])^{-1}$$

where $M(t)$ is size at time t, A is the asymptote, K is the growth-rate constant, and I is age at the inflection point. In a logistic curve the inflection point (i.e. point of maximum growth rate) occurs at ½ asymptotic size. Growth-rate constants and age at inflection points were compared among brood sizes with Tukey's multiple range test (Sokal and Rohlf 1969). We found no differences between the few natural broods of five and those we created, so they were combined in further analyses. A few nests in 1985 were heavily infested with ectoparasitic mites (*Ornithonyssus sylviarum*). As the mites obviously affected growth and survival, we excluded these broods from our analysis (see Briskie and Sealy 1989 for discussion of these nests).

Asymptotic mass was obtained by recapturing fledglings from nests studied earlier. There were no differences in fledgling mass among brood sizes (ANOVA: $F = 0.18$; df = 2, 38; $P = 0.84$), so all data were combined to calculate a single asymptote (10.45 ± 0.11 g, $n = 41$). Asymptotic tarsal lengths were measured on 25 adult Least Flycatcher study skins collected at Delta Marsh and housed in the University of Manitoba Zoology Museum collection. We assumed asymptotic tarsal length was the same for both sexes and for all brood sizes.

We estimated relative survival of young after fledging by using recapture frequencies of banded nestlings known to have fledged. All fledglings were recaptured during routine mist-netting on the study site. Six to 10 nets were run for ca. 6–8 h each day. Nets were set across the entire length of the study area from mid-May through early September each year (except 1987) but netting was not conducted on windy or rainy days. Only fledglings recaptured after 12 days postfledging were included in the analysis as young were still fed by their parents to this age (pers. obs.). Some fledglings remained on the study area up to 40 days after fledging. We assumed all fledglings had an equal probability of being netted and that the proportion of young recaptured from each brood size was an indication of their relative survival. Only a few young return to breed on our study area and we could not determine if brood size affected survival to first breeding.

Analyses followed standard statistical texts (e.g. Sokal and Rohlf 1969). All tests were two-tailed. Standard error of the mean (SE) was calculated for all mean values.

Results

Clutch size.—Least Flycatchers laid two to five eggs per clutch, but four-egg clutches were the most frequent (Table 1). Clutches of five were rare (6.8% of 192 clutches) and restricted to early nesting attempts. Most clutches initiated after the first 2 weeks of the breeding season were renests of nesting attempts that had failed earlier (as indicated by a small sample of marked birds), although at least two nests were known to be second broods (Briskie and Sealy 1987b).

TABLE 1. Least Flycatcher clutch size at Delta Marsh, Manitoba, from 1984 to 1986 combined. Breeding season is divided into five 10-day periods, beginning on day of first clutch initiation.

Days since clutch initiated[1]	Clutch size				Clutch size ($\bar{x}$ ± SE)
	2	3	4	5	
1–10	0	4	81	11	4.07 ± 0.04
11–20	0	10	44	2	3.86 ± 0.06
21–30	0	5	13	0	3.72 ± 0.11
31–40	1	2	6	0	3.56 ± 0.24
After 40	0	6	7	0	3.54 ± 0.14
Total	1	27	151	13	3.92 ± 0.03

[1] Day 1 corresponds to 3 June 1984, 29 May 1985, and 28 May 1986.

A single clutch of two eggs was laid in 1984, but this nest was unusual because earlier the female had incubated a clutch of four nonviable eggs 10 days beyond the normal incubation period (see Briskie and Sealy 1988).

Clutch size did not vary among years (Kruskal-Wallis: $H = 0.90$, df = 2, $P = 0.64$). Clutch size decreased as the season progressed in 1984 (Spearman's rank correlation coefficient: $r = -0.41$, $P = 0.001$, $n = 66$) and 1985 ($r = -0.41$, $P < 0.001$, $n = 87$), but not in 1986 ($r = -0.26$, $P = 0.11$, $n = 39$). Smaller clutches in renests possibly accounted for most of the seasonal decline, although some first nests contained only three eggs. Seasonal decline in clutch size could also reflect a decline in food availability. Once clutch initiation began, arthropod abundance declined over the season in 1984 ($r = -0.85$, $P < 0.001$) and 1986 ($r = -0.70$, $P = 0.008$), but not in 1985 ($r = -0.29$, $P = 0.29$); thus, only in one year did the decrease in food availability coincide with a seasonal decline in clutch size.

Hatching success.—To test whether handling of eggs reduced hatchability, we examined all unhatched eggs in experimental nests for embryonic development. Of 14 experimental nests that survived to hatching, 10 contained unhatched eggs. Embryonic development was apparent in unhatched eggs in 5 of these nests. Moreover, in 5 nests where eggs showed no embryonic development, 3 were laid by the host female. Only in 2 nests did the added eggs neither hatch nor exhibit embryonic development. Excluding these nests from analyses did not affect the outcome; thus, we do not feel our manipulations significantly affected hatchability.

Because only a few natural clutches of five

TABLE 3. Survival of Least Flycatcher nests in relation to clutch size and stage of nesting cycle. Natural and experimental broods of five were combined in analyses. No differences in daily survival probabilities (DSP) were significant.

Nest period	Nests (n)	Failures (n)	DSP ± SE	Estimated success[1] (%)
Incubation				
3 eggs	47	14	0.964 ± 0.0094	64
4 eggs	176	55	0.966 ± 0.0045	67
5 eggs	15	3	0.977 ± 0.0126	76
Nestling				
3 nestlings	59	20	0.960 ± 0.0088	54
4 nestlings	76	16	0.977 ± 0.0055	71
5 nestlings	14	5	0.967 ± 0.0145	61
Combined				
3	74	34	0.962 ± 0.0064	30[2]
4	179	71	0.970 ± 0.0035	38
5	20	8	0.972 ± 0.0097	38

[1] Calculated using egg-laying, incubation, and nestling periods given in Results.

[2] Includes DSP ± SE for egg-laying period: 0.953 ± 0.0098 (188 nests, 22 failures).

TABLE 2. Hatching success in the Least Flycatcher in relation to clutch size. Values from all years combined for unmanipulated clutches. Experimental clutches were from 1987 only.

	Clutch size at hatching				
			5		
	3	4	Unmanipulated	Experimental	Combined
Number of nests	29	75	9	14	23
Clutches with complete hatch (%)	79.3	82.7	55.9	35.7	43.5
Eggs hatching (%)	92.0	95.0	86.7	82.9	84.3
Brood size at hatching ($\bar{x}$ ± SE)	2.76 ± 0.09	3.80 ± 0.04	4.33 ± 0.31	4.14 ± 0.21	4.22 ± 0.16

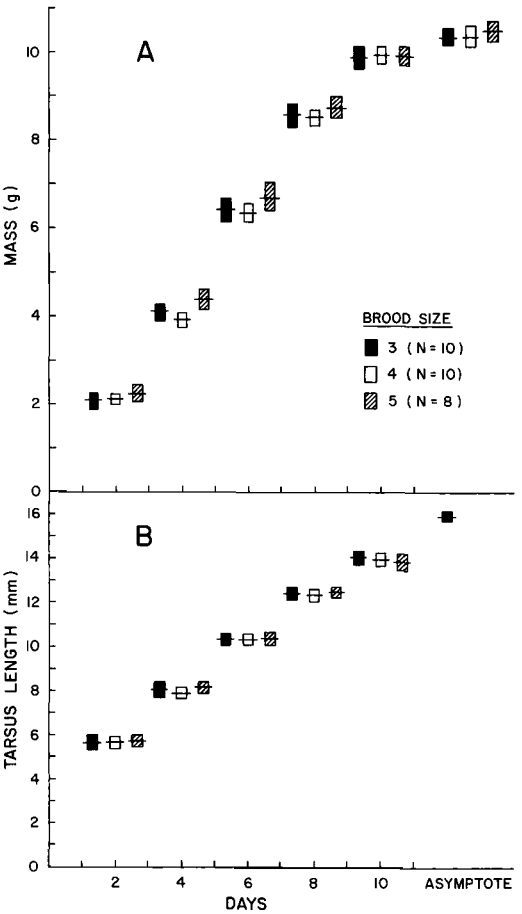

Fig. 2. Growth of Least Flycatchers in broods of three, four and five nestlings for (A) mass and (B) tarsus length. Rectangles are $\bar{x} \pm$ SE. The asymptote for tarsus length represents a composite measure from 25 male and female adult flycatchers collected on the study area. Brood size was not known for these birds.

survived to hatching in a given year, we had to combine control nests from all years. Hatching success did not differ among years in either clutches of four (Kruskal-Wallis: $H = 0.92$, df = 2, $P = 0.63$) or three ($H = 4.9$, df = 2, $P = 0.10$). It is unlikely that combining data from clutches of five introduced any bias to our results. We recorded no differences in hatching success ($\chi^2 = 0.08$, $P > 0.70$) or brood size at hatching (Mann-Whitney: $U = 72.5$, $P > 0.05$) between unmanipulated and experimental clutches of five, and both were combined in further analyses (Table 2).

Number of hatchlings varied with clutch size (Table 2; Kruskal-Wallis: $H = 62.8$, df = 2, $P < 0.001$). Clutches of five produced more hatchlings than clutches of four (Mann-Whitney: $U = 1413$, $z = 2.90$, $P = 0.004$), which in turn produced more than clutches of three ($U = 602$, $z = 7.70$, $P < 0.001$). Although clutches of five produced the most hatchlings, both proportion of eggs hatching per clutch ($\chi^2 = 12.9$, df = 2, $P < 0.01$) and proportion of clutches hatching all eggs ($\chi^2 = 14.7$, df = 2, $P < 0.01$) decreased with increasing clutch size (Table 2).

Nesting success.—Clutch size did not affect either length of incubation (clutches of three: 12.1 ± 0.2 days, $n = 16$; clutches of four: 11.9 ± 0.1, $n = 53$; clutches of five: 11.8 ± 0.2, $n = 6$; Tukey's multiple range test: $P < 0.05$ for all comparisons) or nestling periods (three: 15.2 ± 0.2, $n = 10$; four: 14.8 ± 0.3, $n = 20$; five: 14.8 ± 0.5, $n = 6$; $P < 0.05$ for all comparisons). Clutches of five required longer to lay (4.5 ± 0.3, $n = 4$) than either clutches of four (3.3 ± 0.1, $n = 56$) or three (2.6 ± 0.2, $n = 18$; $P < 0.05$ for all comparisons). Consequently, larger clutches were exposed to potential predators for a greater period.

Daily survival probabilities did not differ among different-sized clutches during either incubation or nestling periods or when both periods were combined (Table 3). When laying period was included, overall estimated nesting success was identical for clutches of four and five, and only slightly less for clutches of three (Table 3).

TABLE 4. Fledgling production in control and experimental Least Flycatcher nests at Delta Marsh, Manitoba. Data from 1985 only.

	Clutch size at laying			Experimental broods of 5
	3	4	5	
Nests (n)	9	33	4	7
Brood size at fledging ($\bar{x} \pm$ SE)	2.78 ± 0.15	3.27 ± 0.14	3.50 ± 0.29	4.71 ± 0.20
Range of brood size at fledging	2–3	1–4	3–4	4–5
Fledglings/nest attempt[1] ($\bar{x}$)	0.83	1.24	1.33	—

[1] Mean brood size at fledging × estimated probability of success from Table 3.

TABLE 5. Growth-rate constants (K) and inflection point estimates (I) for mass and tarsus length of Least Flycatcher nestlings in relation to brood size. Within a column, values with the same letter are not significantly different (Tukey's multiple range test).

	Growth-rate constant ($K \pm$ SE)		Day of inflection point ($I \pm$ SE)	
Brood size	Mass	Tarsus	Mass	Tarsus
3	0.504 ± 0.019 A	0.316 ± 0.009 A	4.93 ± 0.19 A	3.93 ± 0.15 AB
4	0.505 ± 0.018 A	0.314 ± 0.011 A	4.97 ± 0.09 A	3.96 ± 0.09 A
5	0.499 ± 0.022 A	0.327 ± 0.011 A	4.58 ± 0.16 A	3.47 ± 0.18 B

Fledging success.—Brood enlargement experiments were done only in 1985, and data from this year were analyzed separately. Mean brood size at fledging varied with clutch size (Table 4; Kruskal-Wallis: $H = 17.1$, df = 2, $P < 0.001$). Experimental clutches of five produced more offspring than clutches of four (Mann-Whitney: $U = 204$, $z = 3.47$, $P = 0.0005$), which in turn produced more offspring than clutches of three ($U = 132$, $z = 2.05$, $P = 0.04$). Experimentally enlarged broods of five also produced more offspring than natural clutches of five ($U = 119$, $z = 2.75$, $P < 0.01$), but this was the result of lower initial brood sizes at hatching in unmanipulated clutches (see Table 2; all experimental broods began with five hatchlings).

Effect of brood size on growth and survival.—Growth rates (K) did not vary with brood size for either mass or tarsus length (Fig. 2, Table 5). The time to the inflection point (I) in mass was not affected by brood size; however, broods of five reached the inflection point for growth in tarsus length sooner than broods of four (Table 5). This result is opposite to that expected if increased brood size negatively affects growth.

Recapture frequency of young after fledging did not vary significantly with brood size (broods of three: 25.6%, $n = 86$; broods of four: 30.5%, $n = 95$; broods of five: 29.6%, $n = 27$; $\chi^2 = 1.98$, df = 2, $P > 0.05$). We believe that relative survival after fledging was similar in all brood sizes.

DISCUSSION

Experimentally enlarged broods of five produced the most young, which grew and survived as well as young in smaller broods. This suggests that broods of five were the most productive in the dune-ridge forest. However, in all years of our study, four-egg clutches were the most frequent. Contrary to the food-limitation hypothesis, Least Flycatchers did not raise the maximum number of young they could feed during a single nesting attempt. The ability to feed an enlarged brood adequately does not limit clutch size and cannot explain why Least Flycatchers do not lay five eggs more frequently.

Our observations indicated that clutch size was not limited by the ability of females to incubate a larger number of eggs. Least Flycatchers successfully incubated clutches larger than the modal size, and although hatching efficiency declined with both larger natural and experimental clutches, the greatest number of hatchlings was produced from clutches of five. In this respect, Least Flycatchers appear similar to Wood Ducks (*Aix sponsa*, Leopold 1951), American Coots (Fredrickson 1969), Partridges (*Perdix perdix*, Lack 1947), Mourning Doves (Westmoreland and Best 1987), and Fieldfares (Slagsvold 1982b). In these species, the number of hatchlings continues to increase with clutch size beyond the modal size.

Winkler and Walters (1983) suggested recently that the incubation-ability hypothesis applies only to those taxa with truncated clutch-size distributions. For example, many Charadriiformes, which typically lay four eggs, experienced poor hatching success when clutches were increased by one (Hills 1980). Adding a fifth egg resulted in uneven heating of the entire clutch so that any individual egg might be put into a cold position long enough to kill the embryo. Presumably, reducing egg size could increase the ability of birds to cover them, but it might be disadvantageous in those species where larger eggs are required to produce large and precocial young (Andersson 1978). Least Flycatchers lay smaller eggs in clutches of five than they do in either clutches of three or four (Briskie 1985), but hatching success did not vary between natural and experimental five-egg clutches (which were made up of eggs from

three- and four-egg clutches), and this did not seem to be an adaptation to increase incubation efficiency.

The frequency of parental feeding deliveries increased with brood size in Least Flycatchers (Briskie 1985). Consequently, larger broods potentially were in greater jeopardy from predators that respond to parental activities when locating nests (Skutch 1949). Nevertheless, we found little evidence that predation pressure placed an upper limit on clutch size. Although nest predation was the greatest source of breeding failure on our study area, the rate of predation was similar for all clutch sizes.

Limits to clutch size in the Least Flycatcher.— None of the three factors we tested appeared to limit Least Flycatchers to a modal clutch size of four eggs. There are several additional factors which may limit clutch size below the number of young that can be raised.

First, clutches smaller than the most productive might be favored if parents that tend larger clutches experience greater mortality than those with smaller broods (Williams 1966, Charnov and Krebs 1974). The compromise between increased fecundity and decreased adult longevity has been recorded in a few field studies (Askenmo 1979, Nur 1984b), although most have reported little or no discernible relationship (Perrins 1965, Bryant 1979, De Steven 1980, Alerstam and Högstedt 1984), or even a positive relationship between survival and fecundity (Högstedt 1981a, Smith 1981). We did not examine adult survival in Least Flycatchers, so we do not know if larger broods sufficiently decrease adult survival to favor reduced effort at a current breeding attempt. Typically, flycatchers are short-lived birds. The oldest recapture in 6 years of banding was a single 4-yr-old male (S. G. Sealy unpubl. data). Given a short life expectancy, any particular individual will have a low probability of repeated breeding. This suggests that reproductive effort should be near the maximum at a given nesting attempt (Stearns 1976, De Steven 1980).

A second possibility is that optimal clutch size in one year may not necessarily be so the following season (Lack 1966). As a result, the most frequent clutch size is optimal, not for the current breeding attempt, but for previous environmental conditions. Because we performed brood enlargement experiments in 1985 only, we cannot be certain that smaller clutches were not optimal in previous years. However, we feel this possibility was small. Midges have emerged in large numbers during every breeding season since 1974, when work first began in the dune-ridge forest (S. G. Sealy pers. obs.). Arthropod abundance monitored by sweep-net samples over several years also suggests that 1985 was not exceptionally above normal (Busby and Sealy 1979, Biermann 1980, Guinan and Sealy 1987) and, therefore, that Least Flycatchers could probably raise enlarged broods in most years.

Because egg laying requires a substantial energy expenditure (Walsberg 1983), food available to laying females also might limit the number of eggs produced (von Haartman 1971). This hypothesis was applied initially to precocial species (e.g. Ryder 1970), but female condition is known to affect clutch size proximately in some altricial birds (Jones and Ward 1976, Pinowska 1979). For example, birds provisioned with extra food nested earlier, perhaps indicating that breeding was prevented until food availability reached a level when laying became possible (Perrins 1970, Källander 1974, Yom-Tov 1974, Smith et al. 1980). Our observation of a decrease in egg size with clutch size suggests flycatchers may have difficulty producing larger clutches without compromising investment per egg. Nonetheless, only one food-addition experiment on a passerine has documented a significant increase in clutch size (Magpie, *Pica pica*, Högstedt 1981b).

If food availability limited clutch size in Least Flycatchers, one might expect clutches to be larger at Delta Marsh because of the abundance of food created by the large emergences of midges. This did not appear to be the case. We calculated clutch size off the study area from nest-cards filed in the Prairie Nest Records Scheme (PNRS) deposited at the Manitoba Museum of Man and Nature, Winnipeg. Clutch size from nests reported to the PNRS ($\bar{x} = 3.89$, range 3–5, $n = 35$) was not significantly different from that on the study area (see Table 1, Mann-Whitney: $U = 2899$, $z = 0.83$, $P = 0.41$). The area covered by this system included the southern portions of the Canadian Prairie Provinces between approximately 49° and 54° N and 96° and 115° W. Most nests from the PNRS files were located in and around golf courses, suburban yards, city parks, or cottage lots. Although we do not know the availability of arthropods in these areas, the unusual abundance of insect prey at Delta Marsh (Fig. 1) suggests they would be lower. Clutch size in our population in Man-

itoba also did not differ from Least Flycatchers studied by Walkinshaw (1966) in Michigan ($\bar{x}$ = 3.95, range 3–5, n = 46; Mann-Whitney: U = 119, z = 0.56, P = 0.58).

Clearly, both comparisons are only indirect tests of the egg-production hypothesis. It is possible that the food levels necessary for egg production were not limiting in any of the populations under consideration. Ideally, a food-addition experiment would be necessary to test this hypothesis, but this could prove impossible with strictly insectivorous passerines. Alternatively, Hussell and Quinney (1987) correlated changes in clutch size with food availability in the Tree Swallow (*Tachycineta bicolor*) by using several populations and time periods differing in relative prey abundance.

For some species, the upper limit in clutch size may be constrained by nest size (Slagsvold 1982b). Slagsvold found Fieldfares raised more offspring when their original nests were substituted with larger artificial nests. Although open-nesting birds presumably could evolve larger nests, such nests might diminish efficiency of incubation or be more conspicuous to predators (Slagsvold 1982b). As a result, young in clutches larger than the nest can contain will suffer disproportionately higher mortality from trampling or falls. In the Least Flycatcher, we observed losses in three of nine broods of five that could be attributed to overcrowding. In all cases, a few days from fledging, we found young alive on the ground under the nest. These young were the oldest or second-oldest in the two nests in which nestlings were identified. At this stage, nestlings were still flightless, so their chances of survival were probably quite low. In comparison, only 1 nest out of 50 other broods of 3 or 4 experienced a similar loss. Despite this loss, broods of five still gave rise to more surviving offspring than smaller broods (Table 4). Presumably larger clutches should still be favored even with a greater potential of falling.

A final possibility may be the restricted nature of the study site. Although clutches of five were more productive in the dune-ridge forest, this may not be true elsewhere. Dispersal to and from the area is probably quite high. We recaptured <8% of all banded nestlings (n = 240, 1982–1986) in subsequent years through routine mist-netting. Without some degree of isolation, larger clutch sizes simply may not have been able to evolve in this restricted area of abundant food.

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ROLE OF THE PROCTODEAL GLAND FOAM OF MALE JAPANESE QUAIL IN NATURAL COPULATIONS

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ABSTRACT.—Male Japanese Quail (*Coturnix japonica*) produce a thick foam from the proctodeal gland of the cloaca that is mixed with semen and inseminated into the female during copulation. We examined the effect of foam on fertility in natural copulations. In 2-male/5-female mating groups, fertility of intact males was 98% and fertility of males whose proctodeal glands were cauterized (non-foam-producing) was 26%. When an intact male competed with a non-foam-producing male, the intact males sired 99% of the progeny. We demonstrated that the presence of foam, whether artificially placed or naturally placed, extended the duration of fertility of those females fertilized. In copulations without foam, or with artificially placed foam, the proportion of females fertilized decreased significantly compared with copulations by intact males where foam was naturally placed in the proctodeum of the females (and not in the distal part of the oviduct as chicken males do when they inseminate hens).

We believe that foam acts as a medium for sperm transport along the oviduct. Why foam exists in its present form and not as part of seminal fluid, and why the foam-semen mixture is deposited in the proctodeum and not in the distal oviduct, are questions that remain.
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ADULT male Japanese Quail (*Coturnix japonica*, American Ornithologists' Union 1983) and Common Quail (*C. coturnix*) produce a thick foam from the proctodeal gland (King 1981, Klemm et al. 1973) of the cloaca (Coil and Wetherbee 1959, Ikeda and Taji 1954, Nagra et al. 1959). The secretion of the gland is a viscous glycomucoprotein that apparently foams when it interacts with CO_2 and H_2 produced by cloacal bacteria (*Escherichia coli* and *Proteus mirabilis*) that metabolize glucose in the secreted mucoid (McFarland et al. 1968). Although foam production is at present known only in *Coturnix*, a similar glandular tissue has been found in chickens and turkeys (King 1975, 1981; Komarek 1970) and is thought to produce a "frothy fluid" (Fujihara and Nishiyama 1984, Fujihara et al. 1985). The frothy fluid is a lymph-like fluid secreted from surface tissue near the papilla with a negligible amount of foam from the proctodeal gland (Fujihara et al. 1987). There is still controversy as to whether the origin and the function of the glandular tissue in the turkey and chicken are similar (Fujihara et al. 1987, Bakst and Cecil 1986, Lake pers. comm.). Similar tissue has been found in the same area of the cloaca in ducks and geese (Komarek 1971), and Hatch (1983) also found glandular tissue in Northern Fulmar (*Fulmarus glacialis*) which he thought similar to that of the proctodeal gland. The tissue in these species have not developed into functional and foam-producing glands.

The development of the gland and the production of foam in *Coturnix* is dependent on testosterone stimulation (Sachs 1967, Balthazart et al. 1979, Massa et al. 1980). There are several hypotheses regarding the function of the foam. Perez and Juarez (1966) thought it prevented postcopulatory sperm leakage from the female. Renzoni (1968) suggested that foam was a lubricant for the male's phallus. Schleidt and Shalter (1972) argued that foam was used by the male as a territorial marker. No conclusive evidence supports any of these hypotheses (King 1981). Foam is most commonly thought to be an aid to reproduction (Ikeda and Taji 1954, Klemm et al. 1973, McFarland et al. 1968, Ogawa et al. 1974, Wetherbee 1961) because it is passed on to the female along with semen during copulation and its production is testosterone-dependent (Sachs 1969, Adkins 1974). However, Marks and Lepore (1965) and Lepore and Marks (1966) obtained good fertility by artificial insemination without mixing foam with the inseminated semen.

In order to determine the function of foam in reproduction in the Japanese Quail, we studied the effect of foam on fertility under natural

copulations. Subsequently, we generated and tested hypotheses concerning the role foam may play (Cheng et al. 1989).

MATERIALS AND METHODS

Wildtype (UBC-A) and white plumage (UBC-W) Japanese Quail were obtained from the Quail Genetic Stock Centre at the University of British Columbia. White plumage is recessive to wildtype (Roberts et al. 1978) and is used as a genetic marker to determine paternity of progeny from the mating groups. The wildtype and white phenotypes can be distinguished after 10 days of incubation and paternity determined.

EXPERIMENT 1

Birds were raised in mixed sex and genotype groups from hatching until 4 weeks of age. Males were then separated from the females and only white females were maintained for the experiment. At 4 weeks of age, before the proctodeal glands became fully developed and functional, the proctodeal glands of 30 males from each line (UBC-A and UBC-W) were destroyed permanently by electric cautery (Hickman 1984). After application of local anesthetic (Xylocaine), a 1-cm cut was made longitudinally along the midline of the dorsal wall of the cloaca starting from the dorsal lip. Insulated forceps were used to keep the surface exposed, and cautery was done with a hyfrecator operating at 90 volts. Fifteen males from each line were sham-operated. Cauterization was performed rather than surgical removal to minimize distortion of the cloacal area when removing the glands. To test each cauterized male for fertility before the start of the experiment, it was housed with a female (not an experimental bird) for 6 days. Three males from pairs where all the eggs were infertile were not used for the experiment.

At 8 weeks of age, we distributed the experimental birds into 3 replications, each consisting of 4 treatment groups: (1) one cauterized UBC-A male, and one sham-operated UBC-W male, with 5 UBC-W females; (2) one cauterized UBC-W male, and one sham-operated UBC-A male, with 5 UBC-W females; (3) one UBC-A male and one UBC-W male, both cauterized, with 5 UBC-W females; and (4) one UBC-A male and one UBC-W male, both sham-operated, with 5 UBC-W females. Each group was housed in a 122 cm × 92 cm × 46 cm high floor pen with wood shavings litter.

The experiment lasted 8 weeks. To minimize bias due to any particular male, 2 sets of males were used in rotation every 2 weeks so that the first set of males was used during weeks 1, 2, 5, and 6; and the second set was used during weeks 3, 4, 7, and 8. Eggs were collected daily, identified, and incubated artificially in a Jamesway incubator. Phenotypes of the progeny were recorded and the percentage of progeny sired by foam-producing and non-foam-producing males was determined. Fertility, hatchability, and percentage of embryonic death were calculated.

We followed 2 of the 3 replications to determine differences in mating behavior between cauterized and sham-operated males, and between UBC-A and UBC-W males. Eighteen 20-min observations were made on each of the 8 pens. Observations were carried out by the same observer and were divided between the morning, afternoon, and evening periods over the 8 weeks of the experiment. We recorded mating behavior, especially frequency of completed copulations (male bending his tail around the tail of the female with apparent cloacal contact and an obvious thrust of the lower body of the male before dismounting).

Fertility and hatchability data were analyzed by analyses of variance. Mating frequencies were analyzed by ANOVA with repeated measures (Snedecor and Cochran 1980). Because in all treatment groups a UBC-A male was competing with a UBC-W male for the 5 females, their mating behaviors were not independent. Higher frequency of mating activities by one male usually resulted in lower mating frequency of the competing male in the same period. Statistical comparisons of mating frequency between foam-producing and non-foam-producing males were therefore restricted to within-genotype comparisons. Factors entered into the analyses were replications, condition of the male (foam-producing or non-foam-producing), condition of the competing male (foam-producing or non-foam-producing), and all the two-way interactions. Time of day and 3-way interactions involving the time of day were factors in the subplot. All percentages were arcsine transformed before the analyses.

EXPERIMENT 2

Six "fertility-tested," cauterized males and 6 foam-producing (sham-operated) males from each of UBC-A and UBC-W lines were used in staged copulations. In addition, 10 males of each line were maintained for their foam. Thirty-two UBC-W females that were laying infertile eggs were housed in individual 30 cm × 50 cm × 25 cm high wire cages. All the males were caged individually to prevent fighting and homosexual copulations (Adkins 1974).

The experiment consisted of 40 replications of the 4 treatments: (1) female was allowed to copulate with a non-foam-producing male; (2) female was allowed to copulate with a foam-producing male; (3) female was allowed to copulate with a non-foam-producing male and foam was artificially placed in the female's oviduct after copulation; and (4) foam was artificially placed in the female's oviduct and female was then allowed to copulate with a non-foam-producing male.

The experiment was conducted in the evening after the experimental females had laid their eggs. Within 25 min after egg laying, a male of the appropriate

TABLE 1. Fertility, hatchability of fertile eggs, and number of progeny sired by different types of males in the experimental pens. For comparison within column, means followed by different letters are significantly different.

Treatment	Type of UBC-W male	Type of UBC-A male	Eggs set (*n*)	Fertility** (%)	Hatch* (%)	Chicks typed (*n*)	White progeny** (%)
1	foam	foamless	633	76B	74B	418	99D
2	foamless	foam	660	73B	76B	424	1A
3	foamless	foamless	696	26A	53A	109	26B
4	foam	foam	666	98C	70B	540	52C

* $P < 0.05$, ** = $P < 0.01$.

type was placed in the female's cage and remained until a completed copulation occurred. If the male did not make an attempt to mount the female after 15 min, a different male of the same type was used. If two successive males failed to copulate with the female, or if only questionable contacts were made, the female was not used for that replication. After copulation, the male was removed to its own cage. A small sample of the cloacal fluid from the female was obtained with a small vinyl spatula and examined microscopically for sperm. Eggs from the female were collected for the following 10-day period, identified by female and date, and artificially incubated to determine fertility.

Because there were only 32 females available and not all the females were in egg production, females were recycled on the 11th day after the previous copulation. In order to detect any carryover fertility by the previous male, a male of the different line from the previous male was always used. In cases where foam was artificially placed in the female, foam was always obtained from a male of a different line from the male that performed the copulation. Any fertilization as a result of the unlikely contamination of the foam with sperm would then be detected.

The experiment lasted 16 weeks and a total of 40, 35, 40, and 40 copulations were staged for treatments 1, 2, 3, and 4, respectively.

RESULTS

Fertility, hatchability, and progeny phenotypes.—There was no significant difference among the 3 replications in the traits measured in Experiment 1. Fertility was highest in pens where both males produced foam, and lowest in pens where both males did not (Table 1). Hatchability of fertile eggs was significantly lower in pens with two non-foam-producing males. In pens where one male produced foam and one male did not, 99% of the progeny were sired by the foam-producing male. In pens where both males were foam-producing, UBC-W males sired as many progeny as UBC-A males (52% and 48%, respectively), but in pens where both males did not produce foam, UBC-W males sired only 26% of the progeny.

Mating frequencies.—UBC-A males without foam exhibited significantly higher frequencies of mounting attempts and completed copulations compared with UBC-A males that produced foam (Table 2). A significant ($P < 0.05$) time by condition of male interaction indicated that although the frequency of mating attempts by foam producing UBC-A males were significantly lower during the afternoon period, non-foam-producing UBC-A males exhibited high frequencies during all three periods of the day. Other interaction terms were not significant. Whether the competing male produced foam or not had no significant effect on the mating frequency of UBC-A males. The mating frequencies were not significantly different between normal and cauterized UBC-W males. Although the differences were not compared statistically, non-foam-producing UBC-A males attempted and completed about three times as many copulations as non-foam-producing UBC-W males (0.36 vs. 0.12).

TABLE 2. Frequency of mating attempts (MA) and completed copulations (CC) per male per observation period (20 min).

Types	UBC-A male		UBC-W male	
	MA	CC	MA	CC
Foam-producing	0.29*	0.16*	0.18	0.15
Foamless	0.53	0.36	0.19	0.12

* $P < 0.05$, within column comparisons.

Frequency of sperm transfer during copulation.—The frequencies of sperm transfer during copulation by normal and cauterized males were not different (Table 3). We observed sperm in 27 of 64 (42%) cloacal samples obtained from

TABLE 3. Occurrence of sperm transfer during copulations by experimental and normal males.

Treatments	Sperm	No sperm
Non-foam-producing males		
1. Copulation, no foam	11	12
3. Copulation, then foam	8	11
4. Foam, then copulation	8	14
Sham-operated males		
2. Normal copulation	9	9

females after completed copulations with non-foam-producing males. In 18 cloacal fluid samples obtained after completed copulation with a foam-producing male, sperm were observed in 9 (50%).

Foam and fertility.—Fertility in birds can be measured by overall fertility within a certain period, the proportion of females fertilized and, for each female fertilized, the duration of fertility. For an 8-day period after a single copulation, the overall fertility was significantly higher for copulations involving foam, whether natural or artificially placed (45%, 42%, and 40% for treatments 2, 3, and 4, respectively), than copulations without foam (22%) (Table 4).

The proportion of females that laid at least one fertile egg after the copulation in treatments 1, 2, 3, and 4 were 0.1 (4/40), 0.51 (18/35), 0.18 (7/40), and 0.13 (5/40), respectively. Sham-operated males were able to fertilize proportionally more females ($\chi^2 = 9.5$, $P < 0.005$) than cauterized males regardless of timing of artificial placement of foam.

For copulations that involved foam, either natural or artificially placed (treatments 2, 3, and 4), fertility lasted for 7–8 days (Table 4). For copulations without foam (Treatment 1), fertility lasted only 5 days.

Position of the foam in the female after copulation.—During the course of the experiment, we observed that in natural copulations, foam mixed with semen was deposited by intact males in the female proctodeum (Fig. 1). This was confirmed in a separate experiment by injecting a small amount of food color (blue) into the males' proctodeal gland before copulation and sacrificing the females afterwards to examine where the blue foam was deposited and which part of the cloaca was stained (Cheng et al. 1985). Blue foam was found only in the proctodeum of the females, and in no other part of the cloaca or the oviduct. This differs from chickens where the hen everts the distal vagina during copulation and the cock deposits the semen on the exposed portion of the oviduct (Guhl and Fischer 1969).

TABLE 4. Percentage fertility and duration of fertility of eggs laid by females[a] after a single copulation.

Days after copulation	Treatments[b]			
	1	2	3	4
1	0/4[c]	3/14	4/7	1/4
2	3/3	12/14	4/5	4/4
3	1/2	11/15	2/6	3/4
4	0/2	8/14	3/6	2/4
5	1/4	10/16	2/7	0/5
6	0/4	3/17	2/6	3/5
7	0/2	3/14	2/6	1/5
8	0/2	3/13	1/5	0/4
9	0/2	0/11	0/5	0/3
10	0/2	0/13	0/5	0/2
Total (8 days)	5/23	53/117	20/48	14/35
% fertile	22	45	42	40

[a] Females that have laid at least one fertile egg.
[b] 1 = copulation, no foam; 2 = copulation with intact male; 3 = copulation, then foam; 4 = foam, then copulation.
[c] Number of fertile eggs/number of eggs set.

DISCUSSION

We found that in natural copulation, foam affected fertility in three ways. First, the presence of foam, whether placed artificially or naturally, extended the duration of fertility of those females fertilized. Second, in copulations without foam, or with artificially placed foam, the proportion of females fertilized decreased significantly compared with the proportion fertilized in copulations by intact males where foam was placed naturally. The position of the foam deposition, and the mixing of semen and foam during copulation, seemed to be important. Third, the difference in fertility between foam-producing and non-foam-producing males was not because of difference in frequency of sperm transfer. The data were also consistent with the observations that in domestic Japanese Quail, only about 50% of observed completed copulations involved sperm transfer (Adkins 1974).

Ogawa et al. (1974) found that fertility of males whose proctodeal glands were removed surgically was 14.6% compared with 56.5% for controls. Ikeda and Taji (1954) assumed that the foam was part of the seminal fluid, but Lepore and Marks (1966) and Kobayashi et al. (1972)

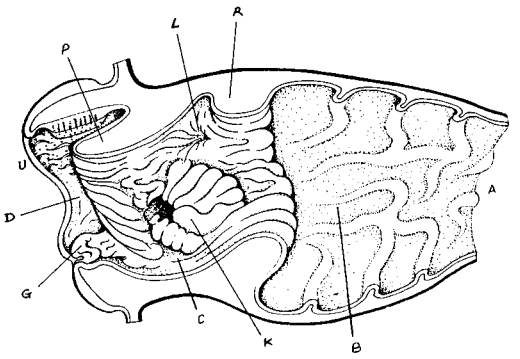

Fig. 1. Cloaca of mature hen: view from the right side. (From Komarek [1971], courtesy of Acta Veterinaria Brno.) (A) rectum; (B) coprodeum; (C) urodeum; (D) proctodeum; (G) clitoris; (K) left oviduct (functional) opens on a rosette-like mound; (L) the ostium of the left ureter; (P) uroproctodeal fold (*plica proctodeourodealis*); (R) coprourodeal fold (*plica urodeocoprodealis*); (U) cloacal opening. Cloaca of mature female Japanese Quail would be similar.

demonstrated that in artificial insemination, where semen was placed in the vagina without foam, the same fertility level was achieved as when semen and foam were mixed.

Without foam, copulation frequency affected fertility. In natural copulations, both fertility and hatchability of fertile eggs was affected adversely by the lack of foam. This indicates that sperm stored in the sperm storage tubules of the females were aged and stale (Nalbandov and Card 1943, Friess et al. 1978). Because foam affected both the proportion of females fertilized and fertility duration, this implies that for copulations by non-foam-producing males, inadequate fresh sperm reached the sperm storage tubules of the females (Van Wambeke 1984). This is consistent with the suggestion (Ikeda and Taji 1954) that foam is a medium for sperm transfer along the oviduct.

We have no explanation for the observation that cauterized UBC-A males exhibited higher mating frequency than intact males of the same genotype, and why this was not observed in UBC-W males. These observations are interesting and deserve to be studied further, but they are not relevant to the role of foam in fertility.

It is possible that the proctodeal gland has developed to play a much more important role in fertilization under domestication where presumably the pressure for fertilizing more females has intensified (Clayton 1972, Haase and Donham 1980). Wild *Coturnix* are mostly monogamous (Wetherbee 1961, Moreau and Wayre 1968, Nichols in prep.). Schleidt and Shalter (1972) reported that the size of the proctodeal glands from captured wild males maintained in the laboratory was much smaller than in domestic strains maintained under identical conditions. The amount of foam that can be squeezed from a wild male's gland was small compared with that obtainable from a domestic male. Similar observations were made by Cheng (unpubl. data) on captive feral Japanese Quail from Hawaii and their captive-reared progeny. Under domestication and with high-density rearing conditions, pair bonds break down and males become promiscuous. Domestic males have the opportunity to fertilize many more females but at the same time face intense competition from other males to fertilize these females (Cheng and Burns 1988). Under these circumstances, the foam gland may enlarge.

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(*continued on p. 291*)

PROCTODEAL GLAND FOAM ENHANCES COMPETITIVE FERTILIZATION IN DOMESTIC JAPANESE QUAIL

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ABSTRACT.—Foam produced by the proctodeal gland of male Japanese Quail (*Coturnix japonica*) may help sperm transportation along the oviduct by inducing higher motility of the sperm via aeration. It is possible that foam can also suspend sperm in the proctodeum of the female to avoid sperm elimination by the egg as it travels down the oviduct. We demonstrated that when quail semen was mixed with foam in vitro, sperm motility was prolonged significantly. We labeled foam with Tc-99m sulfur colloid to demonstrate that foam deposited by the male through natural copulations may be retained by the female for more than 2 h and is not eliminated during oviposition. We concluded that the proctodeal gland of the male Japanese Quail may have evolved to produce a large amount of foam under domestication. This may allow the males to fertilize more females in competition with other males. *Received 29 April 1988, accepted 15 December 1989.*

SEVERAL hypotheses propound the function of proctodeal gland foam of the male Japanese Quail (*Coturnix japonica*) (Perez and Juarez 1966, Renzoni 1968, Schleidt and Shalter 1972), but no conclusive evidence nor a satisfactory explanation has been presented (King 1981). While the presence of foam may not be important for good fertility in artificial insemination where semen has been deposited in the vagina (Lepore and Marks 1966, Kobayashi et al. 1972), it is crucial for achieving good fertility in natural copulations (Cheng et al. 1989), where semen may be deposited in the proctodeum of the female. It is likely that foam acts as a medium for sperm transportation, but the reasons why foam is limited to male *Coturnix* and why the foam-semen mixture is deposited in the proctodeum during copulation remain unclear (Cheng et al. 1989).

Chickens and ducks lay early in the morning (Wilson 1964, Tanabe and Nakamura 1980), turkeys lay mostly during late morning and early afternoon (Wilson 1964), but Japanese Quail lay during the 2–4 h before sunset (Wilson 1964, Konishi 1980). In all these species, ovulation normally occurs 15–75 min after oviposition of the previous egg (Sturkie 1985) and fertilization occurs in 15–30 min after ovulation (Gilbert 1971). Sperm normally take an hour to traverse the oviduct (Allen and Grigg 1957), but near the time of ovulation, sperm can traverse the oviduct in 10–15 min (Bobr et al. 1964b, Howarth 1971). On the other hand, an egg in the oviduct, especially a hard-shelled egg, effectively blocks the sperm (Bobr et al. 1964a). Before shell membranes are deposited around the egg, albumen can also trap sperm and apparently lower the number of sperm stored in the uterovaginal (UV) sperm storage tubules (Bobr et al. 1964a). It is unlikely that sperm would survive in the lumen of the oviduct during periods of albumen and shell secretion (Howarth 1974).

Artificial insemination at times when a hard-shelled egg is in the oviduct results in lowered fertility (Moore and Byerly 1942, Parker 1945, Wyne et al. 1959). Thus a male should copulate within an hour postoviposition to make use of this "insemination window" (Cheng et al. 1983) to optimize his chance of fertilizing an ovum. If he inseminates shortly before oviposition, most of the semen may be carried out by the egg. If he inseminates the hen shortly after oviposition, he has a good chance of fertilizing the next ovum ovulated. If he delays, the ovum is no longer fertilizable and, although the sperm inseminated may be stored in the UV tubules, they are at risk of being covered by semen from other males via subsequent copulations and have little chance of fertilizing subsequent ova. In a flock situation, it may be difficult for a male to determine the egg-laying time for each female or to have the opportunity to copulate with a female at the appropriate time (Cheng and Burns 1988). The male would do best to copulate when most or all of the females in the flock have laid to maximize his chance of fertilization. This must balance with the chance of getting most sperm

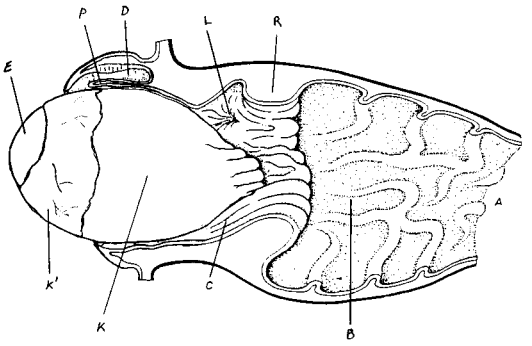

Fig. 1. Schematic illustration of foam-semen mixture position during oviposition (modified from Komarek [1971]; the egg is not drawn to scale): (A) rectum; (B) coprodeum; (C) urodeum; (D) proctodeum, filled with the foam-semen mixture; (E) the exposed blunt end of the egg; (K) left oviduct extended with an egg inside; (K') the everted edge of the oviduct exposing the inside wall; (L) the ostium of the left ureter; (P) uroproctodeal fold (*plica proctodeourodealis*); and (R) coprourodeal fold (*plica urodeocoprodealis*). (See fig. 1, Cheng et al. 1989, for comparison.)

stored by the females for subsequent fertilizations. This prediction is true for chickens (Wood-Gush 1971, Cheng et al. 1985), turkeys (Smyth and Leighton 1953), and ducks (Balthazart and Hendrick 1979, Cheng et al. 1982). In these species, copulation frequencies peak daily near the end of the normal period for egg laying.

In Japanese Quail, the predicted time for copulations would be after dark because egg laying peaks just 2–4 h before dark and some females lay consistently after dark (Wilson and Huang 1962, Opel 1966). Japanese Quail are not active after dark. There is no clear peak in copulation frequency in Japanese Quail and only a significant low that corresponds to the peak of egg-laying activities (Ottinger et al. 1982). It is possible that the foam gland developed in the Japanese Quail because its exudate compensates for the lack of an "insemination window" as occurs in other domestic birds. Foam may act as a medium for suspending sperm in the female's proctodeum (a pocket out of the way of the egg as it is being laid; Fig. 1) to avoid excessive loss of sperm during oviposition. As the foam dissipates, sperm may be released slowly (even after dark) for a better chance of fertilization or storage in the UV tubules, or both. In order to support this hypothesis, it must be shown that foam prolongs sperm motility and that the sperm-foam mixture stays in the female and is not eliminated through egg laying. We determined experimentally if foam would prolong sperm motility in vitro. Subsequently, we examined the length of time foam remained in the female after copulation, and if foam was eliminated by oviposition or defecation.

Materials and Methods

Five wildtype UBC-A males (see Cheng et al. 1989) were obtained from the Quail Genetic Stock Centre and trained for semen collection. We collected semen by the method of Marks and Lepore (1965) with modifications suggested by H. P. Van Krey (pers. comm., Hickman 1984). Foam was squeezed out of the proctodeal gland and eliminated or collected separately before semen was collected.

The experiment consisted of two treatments with two replications for each treatment. In Treatment 1, semen obtained from a male was divided into two portions. One portion was mixed on a microscope slide with about 20 μl of thin albumen from a fresh quail egg and covered with a cover-slip. The second portion was treated the same except a small amount of foam from the same male that provided the semen was added. Slides were observed simultaneously under two microscopes at room temperature. In Treatment 2, we followed the same procedure except that the foam added was a mixture from males other than the male providing the semen. This would determine if foam interacted immunologically to sperm from other males.

Six sexually mature UBC-A males and 12 UBC-A females were maintained for a second experiment. Two weeks before the start of the experiment, we placed the males in individual cages and habituated them to copulating with females (not experimental females) in the cage. The experimental females were also kept in individual cages and the approximate time of egg laying for each female was recorded daily.

We used a Technecium isotope, Tc-99m sulfur colloid (Frosstimage Sulfur Colloid Kit, Frosst Radiopharmaceuticals; Phan and Wasnich 1981) to label the foam. Tc-99m sulfur colloid has been used in human intravenous injection to monitor blood flow and restrictions, and for liver scanning. It has a physical half-life of 6 h. Colloid was used in this experiment because it is not viscous and will not alter the consistency of the foam. It will not irritate the birds as radiopaque substances would, it efficiently adsorbs other substances to its surface, and it is more likely to adhere to the foam. Only a minute quantity is required for labeling.

Radiographic (gamma ray) pictures were taken with a Picker Dyna Camera 4 connected to a Picker Image Programmer and an Adac Laboratories DPS-2800 computer. We monitored images from the camera on

a video screen and recorded them on hard disk for further analyses.

A first trial was conducted as a control to determine if the Tc-99m sulfur colloid adequately labeled the foam. We injected two males each with 0.025 ml (0.05 millicuries) of Tc-99m sulfur colloid directly in the proctodeal gland through the dorsal wall of the cloaca. Radiographic pictures were taken of the males. Then the foam from each male was squeezed out on a petri dish and a picture was taken of the foam alone.

In each additional trial, colloid (0.05 millicuries) was injected into the proctodeal gland of each male and a female was put into the cage with each male. Two completed copulations were allowed to increase the chance of sperm (and foam) transfer. The first 3 females that completed the copulations were used for the trial. We conducted the trials in early afternoons and used females with a hard-shelled egg in the oviduct. In the three trials, a total of 9 females were tested.

After the copulations, we restrained each female on her side on a wire platform with 1" × 2" mesh, with wings folded close to the body and legs stretched. We covered the bird's head with a piece of tissue paper to minimize excitability and stress to the bird. Feathers around the vent were clipped before the trials to minimize interference with the feces in case of defecation. The platform and the bird were placed on the camera stage for gamma ray pictures at regular intervals and after each defecation or oviposition, until about 3 h after the copulations. If the bird defecated, the feces fell through the wire mesh onto a piece of cellophane under the platform so that the feces could be separated to avoid overlapping images on the pictures. We removed the feces and replaced the cellophane before the next picture was taken.

RESULTS

The volume of ejaculate from quail was small (4–7 μl; Buxton and Orcutt 1975) and the semen was thick and viscous. The addition of thin albumen decreased viscosity and increased sperm motility. In all cases where no foam was mixed with the semen, sperm motility slowed 3–5 min after being placed on the slide; motility ceased within 10 min (Table 1). However, when foam was added to the mixture (whether it was foam from the same male that provided the semen or foam from other males), sperm remained vigorously motile even 45 min after they had been placed on the slide. The difference between the slides with and without foam was obvious, and observations ceased after about 45 min. Casual observation on one of the slides with foam added to semen revealed that the sperm were still motile after 95 min at room temperature.

TABLE 1. Duration of quail sperm motility at room temperature.

Treatment	Last observation (min)	Motility
Male 1		
Semen	4	Ceased
Semen + own foam	16	Vigorous
Male 2		
Semen	10	Ceased
Semen + own foam	55	Vigorous
Male 3		
Semen	45	Poor[a]
Semen + others' foam	45	Vigorous
Male 4		
Semen	11	Ceased
Semen + others' foam	45	Vigorous

[a] Small number of sperm with heads in air bubbles trapped under the cover-slip still had slow tail movements. Motility of all others ceased by 8 min.

Results from the trial run confirmed that the injected colloid adsorbed to the foam. When foam was squeezed out of the bird, most of the radioactivity was with the foam and not in the bird.

In 9 females tested, 2 showed very little or no radioactivity. They were probably not inseminated. Of the remaining 7 females, 1 laid an egg while she was restrained on the platform. No foam was observed on the egg. The egg was put beside the bird while a radiograph was taken. Another picture was also taken with the egg alone on the camera stage. No radioactivity was detected on the egg and there was no appreciable loss of radioactivity from the bird. A total of 10 defecations occurred. In 3 of these, no foam was observed on the feces and no radioactivity detected. Again, there was no observable decrease of radioactivity in the birds. In the other 7, radioactive foam was observed on the feces. When foam was observed on the feces, in most cases it retained its original consistency. In two cases where fecal material was liquid, the foam was diluted.

Three of the females lost >50% of radioactivity through defecation by 49, 60, and 51 min after copulation. The intervals for 2 other females were 88 and 145 min, after copulation. The remaining 2 retained the foam through the last observations at 150 and 206 min. The mean time that females retained foam was 107 min.

Discussion

Chicken sperm remains motile for about 25 min at room temperature (Sarvella and Marks 1970). Without mixing with foam from the proctodeal gland, quail sperm in vitro lost motility within minutes after collection. This observation is consistent with that of Ogasawara and Huang (1963). However, with the addition of foam, motility of the sperm was maintained for a much longer period even at room temperature. Schindler and Nevo (1962) reported that aeration of chicken and bull semen generally increased overall motility but decreased the duration of sperm motility. Mixing turkey frothy fluid with turkey semen did not affect sperm motility or fertility (Fujihara et al. 1987). The addition of quail foam to chicken semen did not affect sperm motility (Sarvella and Marks 1970) or may have decreased sperm motility (Hickman 1984). Adding foam to quail semen both increased and prolonged sperm motility, indicating that this is a special reaction in Japanese Quail. Presumably, stimulation by foam facilitates sperm movement into the UV sperm storage tubules once they are in the oviduct, and it lessens the chance of elimination (Lake pers. comm.).

Only one female laid during our trials. Oviposition did not cause the foam and semen mixture to be eliminated from the female body along with the egg. Other females probably delayed oviposition because of the stress of being restrained (Opel 1966). Nevertheless, the single incident of oviposition provided strong evidence that foam in the proctodeum of the female was unaffected by oviposition. Defecation could eliminate some of the foam but foam stayed in females for 2 h or more. The mean time of 107 min was a conservative estimate because birds defecate more often when they are frightened or stressed. Two of the seven females retained all the foam and all of the others had measurable radioactivity at the end of the observation period.

The secretion from the proctodeal gland in wild Common Quail (*C. coturnix*) and Japanese Quail may serve to aerate sperm to facilitate sperm transportation in the oviduct. In domestic Japanese Quail, the proctodeal gland may have further developed to produce a large amount of foam to suspend sperm in the proctodeum of the female away from the path of the egg. Such mechanism would enhance competitive fertilization (Clayton 1972, Haase and Donham 1980) by minimizing sperm loss due to oviposition. In this case, foam may be a neutralizing agent to protect the sperm from the hostile environment (e.g. uric acid and excrement) of the proctodeum, an idea to be explored. If the proctodeum of the female contains foam from a previous copulation, additional deposits from subsequent copulations may have a much higher chance of being eliminated. Under this situation, males which produce more foam per ejaculate would have an advantage. Additional indications that fertilization is highly competitive in males of domestic quail is that they have relatively large testes (2.3% of body mass) and a high daily output of sperm (308×10^6 per bird) (Clulow and Jones 1982).

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The **American Ornithologists' Union** will offer several **Marcia Brady Tucker Travel Awards** to help defray expenses of outstanding students wishing to present a lecture or poster paper at the society's meeting in Pittsburgh. The paper may have multiple authors (not true for best student paper competition; see Call for Papers) but the student's name must be first and the student must present the paper/poster. **Beginning in 1989, no student shall receive more than one MBT Travel Award**; students who have received one past award will be eligible for one more. To apply, send the following material to **Robert M. Zink, Museum of Natural Science, Louisiana State University, Baton Rouge, LA 70803, USA** by **15 May 1989**: (1) expanded abstract of paper, maximum 3 typed double-spaced pages, to include methods, major results, and scientific significance (i.e. not "results will be discussed . . ."; (2) curriculum vitae; (3) anticipated budget of **only travel expenses**; (4) letter of support mailed separately from the academic advisor supervising the research. Note that **10 copies of all materials (except reference letter) must accompany each application.** Applications for MBT awards do not guarantee a place on the scientific program; see instructions given with the Call for Papers in the meeting announcement. Students are expected to present their papers, irrespective of a travel award, if granted a place on the scientific program. Recipients of any A.O.U. research awards during 1989 cannot be considered for MBT funding. The MBT Travel Award competition is separate from competition for best student paper/poster awards (see Call for Papers for rules).

The **20th International Ornithological Congress** will take place in Christchurch, **New Zealand**, on **2-9 December 1990**. The Congress program will include 7 plenary lectures, 48 symposia, contributed papers (spoken and poster), workshops, round-table discussions, and films. There will be a mid-Congress excursion day. Longer tours are planned to interesting ornithological sites in New Zealand before and after the Congress, including the post-Congress cruises to sub-antarctic islands.

The second and final **Circular of the Congress** will be available after 1 October 1989 and will include the registration papers and forms for submitted papers. New Zealand will also host the **20th World Conference of the International Council for Bird Preservation** in Hamilton on **21-27 November 1990** and a **Pacific Festival of Nature Films**, in Dunedin on **27 November** to **1 December 1990**.

Requests for the final circular, which includes information on the above events, should be sent to **Ben D. Bell, Secretary-General, 20th International Ornithological Congress, School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand** (Telex: NZ30882 VUWLIB; Facsimile: NZ 64-4-712070).

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The **Frank M. Chapman Memorial Fund** gives grants in aid of ornithological research and also postdoctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. **Applications are reviewed once a year and must be submitted no later than 15 January, with all supporting material.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA.**

There were no Chapman Fellowships awarded for 1988.

Chapman grants for 1988, totaling $43,954.00, with a mean of $698.00, were awarded to: Juan Amat, moulting ecology of the Red-crested Pochard (*Netta rufina*) in Spain; Gonzalo Arango, la taxonomia y las distribucion del genero *Thamnophilus* en Colombia; Todd W. Arnold, proximate and ultimate constraints on clutch size in American Coots; John M. Bates, winter survivorship in the House Sparrow (*Passer domesticus*): a morphologic and allozymic perspective; Douglas A. Bell, hybridization between the Western Gull and the Glaucous-winged Gull; William L. Benner, range expansion and rapid evolution in the House Finch *Carpodacus mexicanus*; Robert E. Bleiweiss, biochemical systematics of hummingbirds using DNA-DNA hybridization; William I. Boarman, environmental components of selection on avian song; Rhys V. Bowen, evolutionary significance of interspecific foraging competition; Reed Bowman, mediation of asynchronous hatching and brood reduction in White-crowned Pigeons; James V. Briskie, dynamics and consequences of copulation patterns in Smith's Longspur; Neil J. Buckley, role of information transfer in the foraging behavior of Turkey Vultures *Cathartes aura*; Carolee Caffrey, cooperative breeding in American Crows: do helpers help?; Angelo P. Capparella, genetic differentiation among Patagonian birds in secondary contact; Jose Maria Cardosa da Silva, taxonomic studies of birds collected in Urucum and Corumba, Brazil; Kevin Cash, brood reduction in Swainson's Hawk; Glen Chilton, discrimination of dialects by female White-crowned Sparrows; Carla Cicero, variation in the song of the Lincoln's Sparrow (*Melospiza lincolnii*) in California; Thomas Peter Coombs-Hahn, environmental control of reproductive physiology in the Red Crossbill; Donald A. Croll, diving and energetics of the Murre; Timothy Crowe, systematics of Galliformes, Raptors, Bustards and Larks; Robert W. Dickerman, ornithological exploration of Upper Guinea lowland forest refuge; Katherine E. Duffy, the migration of owls at Cape May Point, New Jersey; David Enstrom, continuing investigation of delayed plumage maturation in Orchard Orioles; B. Patricia Escalante-Pilego, geographic variation in *Geothlypis* of Baja, California, and western Mexico; Mary C. Garvin, the role of blood parasites in mechanisms of avian sexual selection; Stephen M. Gatesy, a functional study of avian terrestrial locomotion; Rosemarie Gnam, breeding biology of the Bahama Amazon (*Amazona leucocephala bahamensis*); Pedro C. Gonzales, study of AMNH collection of Palawan birds; Martha Groom, detriments of nesting success and nest-site selection in four beach-nesting bird species; Percy N. Hebert, asynchronous hatching and parental investment in the Yellow Warbler (*Dendroica petechia*); Geoffrey E. Hill, female mate preference in relation to male carotenoid pigmentation in the House Finch; Sylvia Hope, geographic variation in call repertoire of the Steller's Jay; L. Scott Johnson, the function of territorial intrusions and mate guarding in House Wrens; Ian L. Jones, the evolution of social signals of the seabird genus *Aethia*; Michael C. Kaspari, experiments with overwintering mixed species flocks in the Sonoran Desert; Mary Katz, song variation in *Pardalotus striatus*, and its relationship to morphological variation; L. Henry Kermott, ectoparasitism of nestling House Wrens by *Protocalliphora braueri* (Diptera); Nedra Klein, geographic variation and systematics of the Yellow Warbler; Natasha B. Kotliar, a hierarchical concept of patchiness: implications for the foraging behavior of nectarivorous birds; David S. Lee, systematics of seabirds from North Carolina and the Philippines; Bruce Lyon, ecology and evolution of intraspecific brood parasitism in American Coots; Randall J. Mitchell, the effect of nectar rewards on hummingbird behavior and pollen deposition and dispersal; David C. Oren, avifauna of Maranhao State, Brazil; David Pashley, distribution of wood warblers in the Neotropics; A. Townsend Peterson, evolutionary relationships of the *Aphelocoma* Jays; Don Roberson, research on *Pterodroma* in AMNH collection; Frank G. Rozendaal, systematics of Asian-Pacific bush-warblers of the genera *Cettia, Urosphena, Tesia* and *Bradypterus* (Aves: Sylviidae); Karl-L. Schuchmann, behavior and reproduction biology of the Tooth-billed Hummingbird (*Androdon aequatorialis*); Gilles Seutin, mechanism of species

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recognition in the Redpolls; Robert Sheehy, determination of genetic relationships within breeding Harris' Hawks using DNA restriction fragments; Margaret B. Shepard, feeding ecology and social behavior of an endangered Lek Parrot, the New Zealand Kakapo; Cynthia Smeraski, Mount Desert Island Biological Laboratory, Salsbury Cove, ME: Susana Struve, a preliminary study of *Parabuteo unicinctus* in Ecuador; Michelle R. Tennant, mitochondrial DNA variation in birds of the subfamily Picinae; Jean-Claude Thibault, research on Whitney Expedition's journal in AMNH; Christopher B. Thompson, impact of predation on tern populations in Eastern Long Island; Jill M. Trainer, Ontogeny of behavioral cues used in mate choice by Long-tailed Manakins; Joseph and Maria Vagvolgyi, the properties of bird populations at and around hybrid zones, described in the ornithological literature, on the North American continent; Maria P. Velasquez Sandino, frugivorous birds and their relationship with the flora in a very wet tropical forest in San Carlos, Antioquia, Colombia; Peter D. Walsh, the adaptive significance of creching in the Common Eider (*Somateria mollissima*); Dick Watling, investigation of the presence of the Long-legged Warbler on Ovalau, Fiji; Lauren Wentz, aspects of the nocturnal vocal behavior of the Common Loon; Douglas P. Whitfield, mate desertion in the Turnstone *Arenaria interpres;* Yoshika Oniki Willis, study of AMNH collections and bibliography of Mato Grosso birds; Reuven Yosef, the implications of impaling by the Great-grey Shrike (*Lanius excubitor*).

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REVIEWERS FOR *THE AUK*, 1988

The prepublication review process is essential to the maintenance of high scientific standards in a journal. The efforts of the individuals who contributed reviews, both singly and together, are remarkable. Each has been thanked personally, but deserves this public acknowledgment. The memorials for Volume 105 were solicited and managed by C. Stuart Houston. Individuals who contributed two or more manuscript reviews are signified with an asterisk.

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