

FEMALE CHOICE IN MIDDENDORFF'S GRASSHOPPER-WARBLER (*LOCUSTELLA OCHOTENSIS*)

HISASHI NAGATA

Department of Biology, Faculty of Science, Kyushu University 33, Fukuoka 812, Japan

ABSTRACT.—Morphological and territorial factors that influence female mate choice were examined in the monogamous Middendorff's Grasshopper-Warbler (*Locustella ochotensis*) on an islet near Fukuoka, Japan. I assumed that pairing date corresponded with female mate choice. Pairing date was correlated with both territory size and food abundance but was not correlated with selected morphological characteristics of males. Territorial quality was assumed to be correlated with territory size because preferable food resources and nest sites were distributed randomly. I conclude that female mate choice was influenced by territory quality rather than by the morphological characteristics of males. Received 8 July 1985, accepted 28 January 1986.

MORE than 90% of all songbird species are monogamous (Lack 1968), but monogamy only recently has received detailed attention by investigators. Several models of female choice exist for polygynous species (Verner 1964, Orians 1969, Weatherhead and Robertson 1979, Alatalo et al. 1981). The "male deception" hypothesis (Alatalo et al. 1981) cannot be applied to female choice in monogamous species, however, because it explains only why females select already-mated males. The "sexy son" hypothesis (Weatherhead and Robertson 1979) and the "polygyny threshold" model (Verner 1964, Orians 1969) may be potentially applicable. Mating success among males is influenced by male quality in the former model and by territory qualities in the latter. Female choice is expected to play an important role in monogamous species if there are differences in fitness among females. Monogamous females will choose the male with the best territorial or physical characteristics at the time, because delayed mating decreases reproductive success (Perrins and Birkhead 1983). Female choice is difficult to detect, however, in resident monogamous species that have high mate fidelity. Little attention has been paid to mate choice in monogamous species.

I investigated female choice in a monogamous species, Middendorff's Grasshopper-Warbler (*Locustella ochotensis*). The work was designed to assess the relative importance of territorial characteristics that might influence female choice in this species.

STUDY AREA AND METHODS

Middendorff's Grasshopper-Warbler breeds on only six islets in northern Kyushu, Japan. Four (Ohtsukue-jima, Kotsukue-jima, Hashira-jima, and Okitsu-jima) of the six islets are located at the mouth of Hakata Bay. The study was conducted on Okitsu-jima about 10 km north of Fukuoka (130°18'E, 33°41'N) in the vicinity of Shikanoshima Island. A small hill, 16 m high and 0.31 ha in area, is located at the center of the island and is covered with coastal vegetation. The coastal vegetation is divided into a coastal evergreen dwarf-forest, about 4 m in height, dominated by *Pittosporum tobira*, *Lista japonica*, and *Eurya emarginata*; a thicket consisting of *Arundo donax*; and scrub. There are also patches of *Pseudotsuga japonica* shoots. The marginal vegetation is halo-xerophyte dominated by *Angelica kiusiana*, *Carex kobomugi*, and *Boehmeria* sp. (Fig. 1).

There were no predators and no competitors on the islet, and only the Pacific Reef Egret (*Egretta sacra*) and Rufous Turtle-Dove (*Streptopelia orientalis*) bred in the study area. The Great Tit (*Parus major*), Japanese Pygmy Woodpecker (*Dendrocopos kizuki*), and Blue Rockthrush (*Monticola solitarius*) occasionally visited the study area.

The study was conducted from 1981 to 1984. Birds were captured with a mist net and uniquely color-ringed. Twelve males, 9 females, 1 juvenile, and 38 nestlings were banded. The wing length, tail length, culmen length, tarsus length, and lengths of the tenth primary and the second phalange of each banded bird were measured. Nestlings were measured every 1–2 days. Sex was determined by individual behavior after release. Males were identified by their advertising on a song post. Females were identified when they mated with males or carried nest materials. Only females built nests.

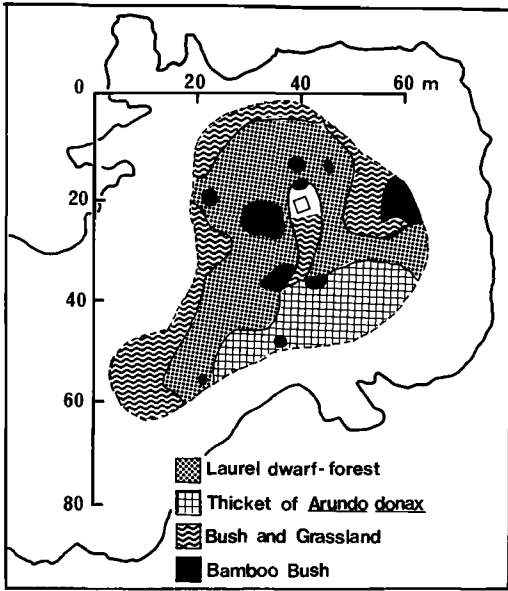


Fig. 1. Vegetation map of Okitsu-jima islet.

I assumed that early pairing leads to increased reproductive success. Therefore, I used pairing date as a measure of mate preference of females. Censuses by line transect were made every 1–2 days beginning in late April of each year. Initiation of pair formation was readily identified by the males' intense courtship and females' solicitation displays.

Territories were determined by the "time mapping method" (Nakamura 1969). Territory was defined in this study as any area defended by advertising, i.e. territory was the convex polygon connecting outer singing points of the owner. The times of observation, locations of individuals, specific behaviors, and vocalizations were recorded.

The abundance of insects and other arthropods was measured at the main study site by the sweep-net method and quadrat sampling of a 25 × 25-cm area, respectively. Twenty strokes of a sweep net in an area of about 1 m² comprised a single sample. All samples were taken on two consecutive days at approximately the same hour. Sampling was conducted every two weeks from May to August in each year. Sampling sites were selected to include representative amounts of each type of vegetation. All arthropod specimens were preserved in 80% ethanol and then sorted, identified to the level of order, and their body lengths measured.

Food items fed to nestlings and fledglings were observed at the sites near the nest through 8× binoculars. To evaluate the quality of territories in terms of food availability, each food item was scored on the basis of Ivlev's electivity index (*E*; Ivlev 1961):

$$E = (r_i - p_i) / (r_i + p_i),$$

TABLE 1. Site fidelity and return ratio of returning birds, 1981–1984.

	Return ratio (%)	Distance (m) shifted between years ($\bar{x} \pm SD$)
Adults		
Males	12/22 (59.1)	7.3 ± 1.54 (<i>n</i> = 12)
Females	7/13 (54.5)	22.5 ± 4.39 (<i>n</i> = 7)
Juveniles	5/24 (20.8)	—

where *r_i* = the relative content of any element in the food items and *p_i* = the relative value of the same element in the food complex of the environment (as a percentage of the whole sweep and quadrat samples). Positive preference was expressed by an index value from +1 to 0, absence of preference by an index value of 0, and negative preference by an index value between 0 and -1. Each food item was scored on the basis of one-half point awarded for each 0.2 interval of an index value, 0 points for no available items (*E* = -1), and 1–5 points for items with an index value between -1 and +1. The food score associated with each territory was calculated by the formula:

$$\text{food score} = \sum (\text{point } i) \times (\text{density } i) \times (\text{size of territory}),$$

where point *i* = the point value of item *i* and density *i* = the density of item *i*.

RESULTS

Middendorff's Grasshopper-Warbler arrives in late spring at northern Kyushu from a wintering area in Southeast Asia. The first influx of males occurred 28 April in 1981, 4 May in 1982, 30 April in 1983, and 8 May in 1984. Females arrived at the breeding site 20 (1983) to 26 days (1984) after the males (for males *n* = 6 in 1983 and 3 in 1984, for females *n* = 6 in 1983 and 7 in 1984). Older birds continued to arrive until mid-June. Yearling males returned to the breeding site around late June. Fifty-seven percent of the adults banded were recovered at breeding sites used in the previous year. There were no differences between the sexes in rates of return (Table 1).

Males established territories shortly after arrival and generally returned to the same territory in consecutive years (Fig. 2). Females usually paired within two days of their arrival. Yearling males did not establish territories in 1982 or 1983, and they disappeared by early

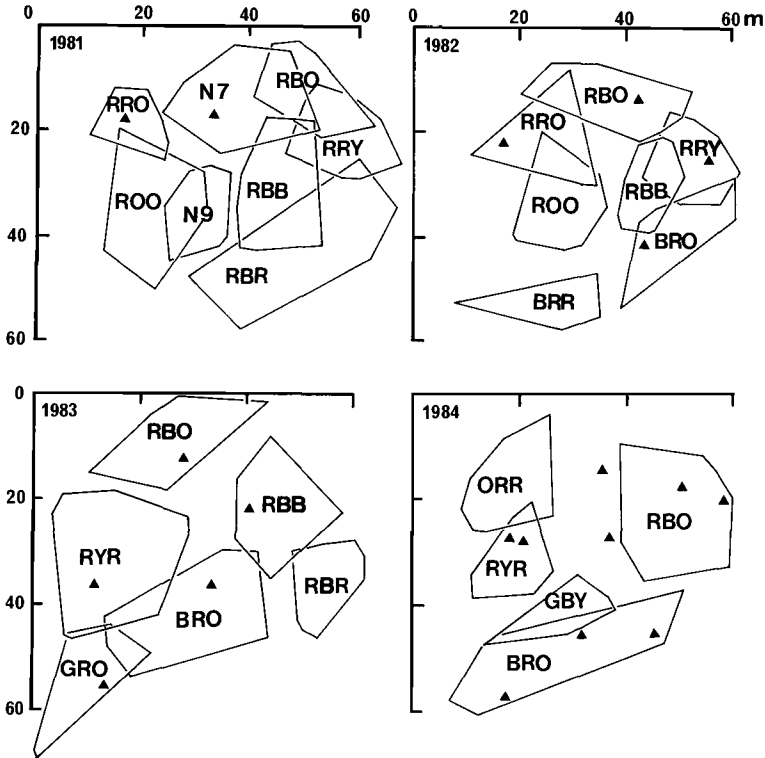


Fig. 2. Territorial arrangement of individual males, 1981-1984. Triangles indicate nest sites. Axes are the same as in Fig. 1.

July. In 1984, however, two yearling males occupied territories in vacant areas between territories of older males. Territorial fidelity was measured as the distance between the center of territories in consecutive years. The annual shift in the ranges for females was significantly larger than that for males ($t_{17} = 3.91, P < 0.05$). Hence, females returned to different territories on the islet, suggesting less strict territorial fidelity (Table 1). Eight banded birds that returned to the same sites in consecutive years changed mates. Mate fidelity was low; only 1 of 7 pairs in which both sexes returned in consecutive years maintained the pair bond. Territory size averaged $310.6 \pm 27.5 \text{ m}^2$ ($\pm \text{SE}, n = 30$) over 4 yr. Territory size increased as population size decreased ($r = -0.83, n = 4, P < 0.20$). The mean territory size in May 1984, when only three males established territories, was $710.7 \pm 69.1 \text{ m}^2$ ($\pm \text{SE}, n = 3$). The mean territory size in 1984 was significantly larger than in other years ($273 \pm 25.3 \text{ m}^2, \pm \text{SE}, n = 25; t_{26} = 5.78, P < 0.001$).

Fledging occurred between late June and early August. Lepidopterans and chilopods (e.g. millipedes and centipedes) were preferred food items in the breeding season (Table 2). These taxa, with homopterans and orthopterans, comprised about 80% of total food items (Table 2). The numbers of lepidopterans collected by sweep sampling were lower than homopterans but were stable throughout the seasons (Fig. 3). The density of soil arthropods (spiders, millipedes, and centipedes) estimated by quadrat sampling fluctuated, but soil arthropods were abundant (Fig. 3). Orthopteran nymphs (grasshoppers, mantids, and cockroaches) appeared in late July, but they were less abundant than lepidopterans and homopterans (Fig. 3). The patterns of changes in food abundance were similar among the three vegetation types (Fig. 3). The preferred dietary items (lepidopterans, orthopterans, and chilopods) were distributed randomly in late May 1984 (Table 2).

The food score for each territory in 1983 increased gradually until late June and decreased

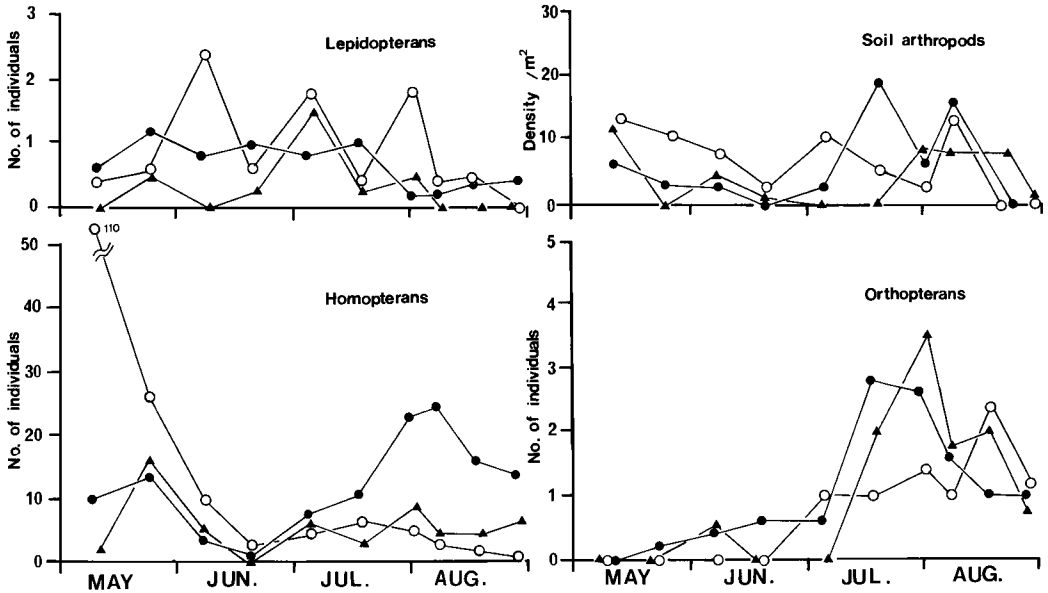


Fig. 3. Seasonal changes in arthropod abundance in 1984. Open circles represent the laurel dwarf-forest, closed circles represent the bush and grassland, and closed triangles represent the *Arundo donax* thicket.

thereafter (Fig. 4). The seasonal change in this derived measure was bimodal in 1984, with peaks in late May and early July. The first peak appeared to be the consequence of large territories because almost the entire area was occupied by only three males. Each possessed a large territory during May 1984. The nestling period started when food abundance became high.

Morphological variation among mates was tested with respect to several characters, but no significant correlations were found (wing length: $r = 0.47, n = 12$; tail length: $r = 0.29, n = 12$; culmen length: $r = -0.25, n = 12$; tarsus

length: $r = 0.05, n = 12$; body mass: $r = 0.29, n = 7$). I conclude that there was no assortative mating in this species. There was no correlation between the pairing date and wing length (Kendall's rank correlation coefficient, $\tau = -0.44, n = 9, NS$), tail length ($\tau = -0.33, n = 9, NS$), culmen length ($\tau = 0.06, n = 9, NS$), tarsus length ($\tau = 0.17, n = 9, NS$), and body mass ($\tau = 0.22, n = 9, NS$). There was no significant correlation between the pairing date and time spent by males feeding fledglings ($\tau = -0.38, n = 8, NS$). Thus, females did not employ these physical characters as relevant cues in mate choice and did not always select dili-

TABLE 2. Diet of *Locustella ochotensis* and its food preference. Asterisks indicate significant clump patterns ($P < 0.05$).

Food item	Percentage of dietary items ($n = 73$)	Percentage of sweep sample ($n = 4,771$)	Preference (Ivlev's index, E_i)	Food point	Index of dispersion in late May (σ^2/\bar{x})
Lepidopterans	32.9	1.8	0.90	5.0	0.82
Homopterans	15.1	30.3	-0.34	2.0	37.87*
Orthopterans	9.6	2.1	0.64	4.5	1.00
Dipterans	6.8	20.1	-0.49	1.5	2.96*
Ephemeropterans	2.7	0.3	0.78	4.5	—
Chilopods	21.9	0.7	0.94	5.0	0.71
Wood lice	5.5	14.7	-0.46	1.5	9.55*
Spiders	5.5	6.1	-0.06	2.5	4.46*

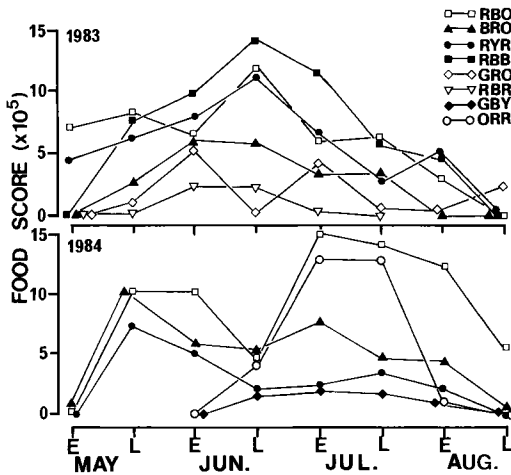


Fig. 4. Seasonal changes in food abundance at each territory in 1983 and 1984. See text for details.

gent males. There was also no correlation between pairing date and the age of males ($\tau = -0.11$, $n = 9$, NS). Yearling males, however, were excluded from breeding because they arrived after all the females had mated.

Correlations were tested among pairing date, fledging date, territory size, food score, arrival date, and the area of bamboo bush that constituted the main nesting site. To combine data from different years, arrival and pairing dates were standardized by using the median dates. There was a weak correlation between the arrival date of males and pairing date ($\tau = 0.56$, $n = 9$, $P < 0.05$) (Table 3). There was no correlation between arrival date and departure date in the previous season ($\tau = -0.13$, $n = 14$, NS).

Pairing date was associated significantly with territory size ($\tau = -0.78$, $n = 9$, $P < 0.01$) and food score ($\tau = -0.69$, $n = 9$, $P < 0.05$). Food scores in late May were associated with those

in mid-July ($\tau = 0.67$, $n = 9$, $P < 0.05$). Hence, relative territory rank did not change throughout the breeding season, because the feeding areas were not different between the periods. The area of bamboo bush was not correlated with pairing date ($\tau = -0.47$, $n = 9$, NS). When food score was held constant, territory size showed a weak correlation with pairing date (Kendall's partial rank correlation coefficient, $\phi = -0.55$). When the area of bamboo bush was held constant, territory size showed a stronger correlation with pairing date ($\phi = -0.71$). When territory size was held constant, however, pairing date showed weaker correlations with food score ($\phi = -0.28$) and the area of bamboo bush ($\phi = 0.15$). These partial correlations suggest that pairing date was correlated primarily with territory size. In accordance with a step-wise multiple regression, variations in territory size accounted for 77% of the variance in pairing dates, variations in male arrival date accounted for 8%, and variations in food score accounted for only 2% of the residual variance (Table 4).

Pairing date was highly correlated with the fledging date of the first brood ($\tau = 0.78$, $n = 9$, $P < 0.01$). Female departure date was correlated closely with fledging dates ($\tau = 0.56$, $n = 9$, $P \leq 0.05$). Thus, early breeding and early departure followed early pairing. Young that fledged before August received care for longer periods than those that fledged in August [early fledglings: 20.3 ± 5.1 days ($\bar{x} \pm SE$), $n = 10$; late fledglings: 12.0 ± 2.8 days, $n = 5$; Mann-Whitney U -test, $P < 0.01$].

DISCUSSION

Generally, it is assumed that males with good territories or good physical attributes acquire a mate early in the breeding season. Early mating enhances reproductive success for two rea-

TABLE 3. Correlation between six variables potentially affecting breeding. Kendall's rank correlation coefficients (τ) are below the diagonal and correlation coefficients (r) are above the diagonal.*

	Pairing date	Arrival date	Fledging date	Territory size	Food score	Area of bamboo bush
Pairing	—	0.73*	0.89**	-0.88**	-0.86**	-0.44
Arrival	0.56*	—	0.79**	-0.58	-0.67*	-0.26
Fledging	0.78**	0.51	—	-0.84**	-0.78**	-0.34
Territory	-0.78**	-0.38	-0.64*	—	0.83**	0.57
Food score	-0.69*	-0.38	-0.56*	0.73**	—	0.46
Bamboo bush	-0.47	-0.07	-0.33	0.69*	0.51	—

* * = $P \leq 0.05$, ** = $P < 0.01$ ($n = 9$).

TABLE 4. Step-wise multiple regression using pairing date as a dependent variable ($n = 10$).

Step no.	Independent variable	r	r^2	Increase in r^2
1	Territory size	0.88	0.77	0.77
2	Male arrival date	0.92	0.85	0.08
3	Food score	0.93	0.87	0.02
4	Area of bamboo bush	0.93	0.87	0.00

sons. First, early pair formation leads to early fledging. If young fledge in June, then females may rear additional clutches. Indeed, pairs with successful nestings in late June in 1984 started a second clutch, although Middendorff's Grasshopper-Warbler rears only one brood in most years. Second, early fledglings were cared for longer. This results in larger and better-developed fledglings and reduced offspring mortality. The duration of parental care depended on the onset of breeding, and all males fed nestlings and fledglings. Therefore, the duration of parental care did not correlate with the starting date of pair formation.

If the difference in mating success among males is large, females will choose "sexy" males (Weatherhead and Robertson 1979). This is not the case in *L. ochotensis* because most territorial males acquired females.

Mating success was correlated with body size in Cetti's Warblers (*Cettia cetti*; Bibby 1982), but I found no correlation between body size and pairing date in Middendorff's Grasshopper-Warbler. Hence, female mate choice was not influenced by physical attributes of male quality.

Based on the strong partial correlation between territory size and pairing date, I conclude that females preferentially choose males with larger territories. Females apparently use territory quality, not age, as a cue for mate choice. Older males acquire more females in Pied Flycatchers (*Ficedula hypoleuca*; Alatalo et al. 1984) and Red-winged Blackbirds (*Agelaius phoeniceus*; Yasukawa et al. 1980). Female Middendorff's Grasshopper-Warblers did not choose older males, however, as indicated by the lack of correlation between pairing date and the age of adult male.

A large territory contains many potential nest sites and abundant food resources. Vegetation structure affects nest sites, especially light pen-

etration to ground level, and may be an important factor (Pleszczynska 1978) in female choice. It was not in *L. ochotensis*, however, as there was only a weak correlation between the area of bamboo bush and pairing date (Table 4). Nest sites were not constrained on Okitsu-jima islet, because Middendorff's Grasshopper-Warbler inhabited a laurel forest and built cup-shaped nests on the twigs. Moreover, nests were free from predation in the absence of predators on this islet. The abundance of food resources correlated highly with territory sizes in Middendorff's Grasshopper-Warbler, because the spatial distribution of preferable dietary items was relatively random (Table 2). Female choice was influenced more by food resources than by nest sites. Apparently, it is a better strategy for female warblers to mate with males on large territories soon after arrival and to breed early. Females thereby maximize their reproductive success in one season.

ACKNOWLEDGMENTS

I express gratitude and indebtedness to Prof. Y. Ono and Dr. K. Eguchi, Kyushu University, for advice, valuable criticism, and suggestions; to Dr. S. Yamagishi, Dr. K. Ueda, and Mr. E. Urano, Osaka City University, for critical comments on the manuscript; and to Dr. A. Buchmann, Tasmanian University, for editing the manuscript and providing many helpful comments. The members of the Laboratory of Ecology, Department of Biology, Faculty of Science, Kyushu University helped in the field survey and offered valuable advice. This work was supported in part by a Grant-in-Aid for Special Project Research on Biological Aspects of Optimal Strategy and Social Structure from the Japan Ministry of Education, Science and Culture.

LITERATURE CITED

- ALATALO, R. V., A. CARLSON, A. LUNDBURG, & S. ULFSTRAND. 1981. The conflict between male polygyny and female monogamy: the case of the Pied Flycatcher *Ficedula hypoleuca*. *Amer. Natur.* 117: 738-753.
- , A. LUNDBURG, & K. STAHLBRANDT. 1984. Female mate choice in the Pied Flycatcher *Ficedula hypoleuca*. *Behav. Ecol. Sociobiol.* 14: 253-261.
- BIBBY, C. J. 1982. Polygyny and breeding ecology of the Cetti's Warbler *Cettia cetti*. *Ibis* 124: 288-301.
- IVLEV, V. S. 1961. *Experimental ecology of the feeding of fishes*. New Haven, Connecticut, Yale Univ. Press.

- LACK, D. 1968. Ecological adaptation for breeding in birds. London, Methuen.
- NAKAMURA, T. 1969. Structure of flock home-range in the Long-tailed Tit. I. Winter flock, its home range and territory. Misc. Rept. Yamashina Inst. Ornithol. 5: 433-461.
- ORIAN, G. H. 1969. On the evolution of mating systems in birds and mammals. Amer. Natur. 103: 589-603.
- PERRINS, C. M., & T. R. BIRKHEAD. 1983. Avian ecology. New York, Chapman & Hall.
- PLESZCZYNSKA, W. K. 1978. Microgeographic predication of polygyny in the Lark Bunting. Science 201: 935-937.
- VERNER, J. 1964. The evolution of polygamy in the Long-billed Marsh Wren. Evolution 18: 252-261.
- WEATHERHEAD, P. J., & R. J. ROBERTSON. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis." Amer. Natur. 113: 201-208.
- YASUKAWA, K., J. L. BLANK, & C. B. PATTERSON. 1980. Song repertoires and sexual selection in the Red-winged Blackbird. Behav. Ecol. Sociobiol. 7: 232-238.

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 should be submitted (in duplicate) no later than January 15th - with all supporting material. Application forms may be obtained from the Frank M. Chapman Memorial Fund Committee, c/o Jane Connelly, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192.

Chapman grants during 1986, totalling \$35,717.00, with a mean of \$576.08, were awarded to: Michael L. Avery, Post-breeding territoriality and foraging in Costa's Hummingbirds; Lenir Alda do Rosario Bege, Estudo da biologia de *Sula leucogaster* e *Fregata magnificens* atraves do anilhamento; Craig Louis Berman, Tactics of intraspecific brood parasitism in the House Sparrow (*Passer domesticus*); Dr. Keith L. Bildstein, Use of museum specimens to test RSD hypotheses in raptors; Janet S. Boe, Colony and nest site selection by Eared Grebes; Bonnie Sue Bowen, Genetic structure and paternity in communally breeding jays; Randall Breitwisch, Mate choice, parental care, and sexual selection in a monogamous passerine, the Northern Mockingbird (*Mimus polyglottos*); Dr. Michael de Leighton Brooke, Assessment of the night vision capabilities of Gough Island Petrels; Albert E. Burchsted, Song dialect interpretation of range expansions of the House Finch on Cape Cod; Dale H. Clayton, Experimental study of avian-ectoparasite coevolution; Thomas I. Crossman, Habitat characteristics of Savannah and Grasshopper sparrows in Connecticut; Michael D. Dennison, Morphological and ecological evolution of Chaffinches; Emile D. DeVito, Fine-grained landscape heterogeneity within a forest ecosystem: effects on the habitat use and distribution of birds; Robert M. Dickerman, Morphological variation in interface zone of the subspecies of Great Blue Heron; Susan Leigh Earnst, The behavior and energetics of polyandrous Red Phalaropes; Carl Edelstam, Molt in large birds of prey and owls; and Mimicry in birds; Marit Evans-Layng, The influence of visual and acoustic stimuli on the kinship preference of female Zebra Finches (*Taenopygia guttata*); Greg Hunt Farley, Comparative breeding strategies of two coexisting passerines: Bell's Vireo and Bewick's Wren; Dr. Julian Ford, Phylogenetic studies on Australo-Papuan birds and some studies on hybrid zones; Charles M. Francis, The growth and development of nestling swiftlets; John A. Gerwin, Relationships of species and genera of hummingbirds: a biochemical perspective; Rosemarie Gnam, Breeding biology of the Bahama Parrot (*Amazona leucocephala*); Jeffrey G. Groth, Systematics of the North American *Loxia curvirostra* complex; Lisa Guminski, The breeding behavior of the White-cheeked Pintail in the Bahamas; Shannon Hackett, Evolutionary genetics of shorebirds: relationships of genera and families; Brian Thomas Henen, *In vivo* determination of body lipid content using cyclopropane gas; James D. Hengeveld, Does the starvation of Red-winged Blackbird (*Agelaius phoeniceus*) nestlings benefit the surviving nest mates?; Geoffrey E. Hill, The reproductive consequences of subadult plumage in male Black-headed Grosbeaks; Kelly M. Hogan, Foraging behavior of fledgling Bat Falcons (*Falco rufigularis*); Torgeir S. Johnsen, The influence of plasma testosterone levels and territorial experience on male behavior and reproductive biology in the Red-winged Blackbird; Mark J. Kasprzyk, Estimates of turnover rates for Semipalmated Sandpipers; Catherine P. Kittleman, Parameters influencing the absence of parasitism on the Yellow-headed Blackbird; David Lemmon, Social dominance and scanning behavior in Black-capped Chickadees (*Parus atricapillus*); William S. Longland, Great Horned Owl predation and predator avoidance by desert rodents; Paul M. Mayer, Population ecology of the Piping Plover in the northern Great Plains; Mara A. McDonald, The evolution and biology of Hispaniolan Palm Tanagers, genus *Phaenioophilus*; Dona J. Milinkovich, Variation in the reproductive characteristics and reproductive success of the House Wren (*Troglodytes aedon*); Randall J. Mitchell, Mechanisms of competition for pollination; David C. Morimoto, Avian community structure in