CONFIDENCE OF PATERNITY AND PARENTAL EFFORT IN RAZORBILLS

RICHARD H. WAGNER[1]

Edward Grey Institute of Field Ornithology, South Parks Road, Oxford OX1 3PS, United Kingdom

ABSTRACT.—I quantified parental effort in biparentally caring Razorbills (*Alca torda*) to test whether variation in male effort was related to variation in their mates' receptivity to extra-pair copulations. On average, males contributed approximately equally to their mates in chick feedings and overnight nest attendance. There was, however, marked variation in relative male effort, with the proportion of male feeding relative to their mates' feeding ranging from 16 to 72%. No significant portion of this variation was explained by direct and indirect measures of males' confidence of paternity. Support was equivocal for an alternative hypothesis, that variation in male effort is caused by differential male ability. Male care increased significantly with fighting ability and mating arena attendance, but not with five other measures of male "vigor." I propose a second alternative hypothesis—that Razorbills and other long-lived, breeding-site-faithful species may reduce their social status over the long term by provisioning poorly, and that lowered status may decrease fitness. Thus, circumstances may exist under which it is beneficial for males to provide care for offspring that may not be their own. *Received 22 April 1991, accepted 10 February 1992.*

ALTHOUGH many species of monogamous birds perform extra-pair copulations (EPCs; McKinney et al. 1984, Birkhead et al. 1987, Westneat et al. 1990), males in most species provide parental care (Wittenberger and Tilson 1980, Oring 1982). The growing evidence that EPCs often succeed in fertilizing eggs (Sherman and Morton 1988, Morton et al. 1990, Westneat 1990) poses a problem in that individuals should be adapted to avoid investing in unrelated offspring (Trivers 1972, Werren et al. 1980). It has been suggested that when males risk losing paternity, they should invest parentally in proportion to their probability of siring their mates' young (Trivers 1972, Maynard Smith 1977, Craig and Jamieson 1985), a prediction I refer to as the "confidence-of-paternity hypothesis."

I tested this hypothesis with monogamous Razorbills (*Alca torda*) in which a high percentage of females actively seek EPCs (Wagner 1992a), even though females require parental assistance from the male. Biparental care is necessary in Razorbills because the chick cannot be left unattended, as it requires brooding (Harris and Birkhead 1985), and because in open sites the chick is very vulnerable to predation (Hudson 1982). Evidence that a single parent

may be unable to provide sufficient food for a chick was suggested in an experiment that showed that two parents had difficulty feeding two young (Lloyd 1977).

Confidence of paternity may be estimated directly by quantifying relevant behaviors in which the male participated or witnessed (Møller 1988), such as the number of EPC attempts involving his mate in his presence. The number of within-pair copulations (WPCs) a male achieves also may affect his confidence of paternity (Møller 1988), because the outcome of sperm competition (in domestic fowl) is known to be influenced by the relative quantity of sperm of each male stored by females (Martin et al. 1974).

Confidence of paternity also may be estimated indirectly by analyzing the receptivity of females to EPCs witnessed by the observer, but not necessarily by the male, such as the number of EPCs the female accepted, or the total number of EPC attempts males made with the female. Female Razorbills were found to vary considerably in the number of EPCs they accepted (0–7; Wagner 1992a), with 50% of females accepting at least one EPC (Wagner 1991a). Females also varied markedly in their receptivity to EPC, accepting EPCs during 0 to 100% of their opportunities (Wagner 1992a).

Two measurable forms of parental effort, chick feeding and overnight nest attendance, appear to be costly to Razorbills. The expense of over-

[1] Present address: Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D. C. 20008, USA.

night attendance is suggested by the extreme reluctance of Razorbills to roost in the colony. Razorbills spend most of their lives at sea and only arrive ashore to reproduce. During the prelaying period, I have never observed them to spend a night in the nest, despite intense competition for breeding sites (Wagner 1991a). Even after the egg is laid, only one parent remains in the nest and, in three years of study, I have never observed more than one parent in the nest overnight. This finding is similar to that of Harris and Wanless (1986), who reported that one parent always roosted at sea during the nestling period. Unlike most species of land birds, whose food sources are often located near their nests, many colonial seabirds travel long distances to forage. The Razorbill parent who remains in the nest overnight is unable to feed either in the evening or early morning, and is dependent upon its partner to relieve it.

Chick feeding appears to be especially costly to Razorbills, whose reproductive strategy is adapted to reduce the number of forays between the colony and the feeding grounds. Foraging distances often may exceed 15 km (S. Wanless, pers. comm.), and Razorbill chicks only receive two to five feedings per day (Lloyd 1976, Harris and Wanless 1986). Razorbills suffer a trade-off between swimming and flying; while their short wings adapt them to pursue fish underwater, they also result in extremely high wing loading (Pennycuick 1987), probably making flight energetically expensive. An apparent adaptation to this pressure is the production of a relatively large egg, from which hatches a semiprecocial chick (Cramp 1985) that develops rapidly and is escorted to the feeding grounds before it attains 30% of adult body weight (Barret 1984). The male is the parent that escorts and provisions the young at sea for several weeks until it is self sufficient (Harris and Birkhead 1985).

METHODS

I studied Razorbills at the Basin colony on Skomer Island, Wales, United Kingdom (51°40′N, 05°15′W) from 1987 through 1989. The data presented in this paper were collected in 1989 from two phases of the breeding cycle. During the prelaying period, I observed copulations; in the postlaying period, I recorded parental activities.

Prelaying period.—Most copulations in the study population were performed in two mating arenas out-side the main breeding colony (Wagner 1991a), which were attended by all 37 pairs whose parental activities were subsequently observed in the colony. Of the 74 individuals comprising these pairs, 63 were color banded. The mating arenas consisted of horizontal ledges 3 m apart, and their proximity to each other allowed for their simultaneous observation. I observed the arenas every morning from 1 April to 20 May and on 22 and 26 May for a mean of 3 h per day (range 1–5 h) and a total of 125 h. I watched from a blind at a distance of 25 m with a 20–60 zoom telescope, beginning at first light (ca. 0500), usually before any Razorbills had arrived from roosting at sea, and continuing until most or all Razorbills had departed from the arenas, or until their mating activities had virtually ceased (usually before 1000). I recorded the time of arrival (or first sighting) of each marked bird, and later calculated mean arrival times (as the number of minutes after 0000) for individuals who attended on at least 10 days.

For all copulation attempts, I recorded the individuals involved and whether or not the copulation was successful. Successful copulations were those in which the male achieved cloacal contact with the female and, presumably, insemination. Males required the cooperation of females, who could reject cloacal contact by pressing down their relatively long, stiff tails and/or by remaining in an upright position, preventing the male from balancing (Wagner 1991b). An extra-pair copulation (EPC) was defined as a potentially fertilizable copulation between a paired female and a male who was not her mate. I considered EPCs to be potentially fertilizable if they occurred prior to egg laying, and if they included cloacal contact.

It was easy to distinguish EPCs from within-pair copulations (WPCs) because pair members were well known from repeated observation. Throughout most of the female's prelaying period, the male and female often arrived simultaneously and consistently attended the arenas together, sitting side by side and allopreening. Mates also copulated frequently, with pairs averaging approximately 50 copulation attempts in the arenas during the 30 days prior to egg laying (Wagner 1991a). The identities of most pairs were confirmed by observation in the breeding colony, where males and females presumed to be mates in the arenas, also shared nesting duties.

Males fight frequently and aggressively in competition for EPCs (Wagner 1991c). "Fights" were rapid bouts of aggression between two individuals, in which one bird lunged at another with its bill. A male was assigned a win if he displaced his opponent, or if he succeeded in stabbing him with his bill without receiving retaliation. Percentage of fights won by males was calculated for males with a minimum of six fights (wins plus losses; Wagner 1992b).

Egg-laying dates were recorded from daily inspections in the colony of those breeding sites that were visible through a telescope. For enclosed sites (e.g.

TABLE 1. Percentage of nights in which the male attended nest during incubation and nestling periods (23 pairs). Mean ± SD (range).

Incubation period	Nestling period	Total
51.1 ± 23.6 (10–100)	51.4 ± 15.6 (18–73)	50.7 ± 15.9 (22–78)

those under boulders), laying dates were calculated by subtracting the mean incubation period of 34 days (Wagner 1991a) from the date of hatching; the hatching date was determined during daily feeding watches, and was assumed to be the first day on which a fish was brought to the nest to feed the hatchling.

Parental effort.—I observed Razorbill nest attendance and feeding in the colony daily from 4 June to 1 July 1989. Observations commenced at first light (ca. 0430) and continued for at least 3 h after the first feeding. Two field assistants (Mark Linfield and Stuart Perry) aided in feeding watches from 19 June to 1 July. They recorded feedings in two sections of the colony for 3 h in the morning (0500–0800 and 0800–1100) and three hours in the afternoon (ca. 1300–1600). Altogether, we observed the colony for approximately 200 observer hours. A total of 37 numbered nests in which one or both adults were banded was visible in the two sections, 27 nests in one and 10 in the other, of which approximately one-half contained chicks on an average day.

For each feeding, the following were recorded: (1) time; (2) nest number; (3) identity of the feeder; (4) species of fish; (5) number of fish; and (6) length of the fish (an average for the load), expressed as the proportion of the bill length (i.e. gape length). An estimate of the weight of each load was calculated by: (a) multiplying mean male or female bill length (53.9 and 52.3 mm; Wagner, unpubl. data) by fish length; then (b) converting length (L) to weight using appropriate formula derived by Harris and Hislop (1978), which for sandeels (*Ammodytes* sp.) is $0.00209L^{3.148}$, and for sprats (*Sprattus sprattus*) is $0.009708L^{2.855}$; and (c) multiplying the number of fish in the load by the

calculated weight of each fish. The three observers were consistent in estimating fish lengths, and there was only a 1% difference in mean estimates among the three of us. There was, however, a 19% and 26% difference between my mean count of the numbers of fish carried, and the mean counts of the other two observers. This was apparently due to observer bias and, in order to remove this source of error from the analyses, I standardized the counts of the other observers against my own.

To measure overnight nest attendance, I identified the mate that was present with the egg or chick overnight at first light, which was usually 15 to 30 min before birds began to arrive. For open sites, the contents of which were visible through a telescope, I identified the individual in the nest, and for enclosed sites (e.g. those underneath boulders), I recorded the mate that arrived and assumed that its partner was inside the nest. This was usually confirmed by the subsequent departure of the presumed overnight attendant.

Relative male effort was calculated for nests in which a minimum of 15 observations were made. All variables in the form of percentages were arcsine transformed for analysis.

RESULTS

To compare the amount of parental effort made by males relative to their mates, I examined the proportion contributed by each sex to: (a) overnight nest attendance; (b) feeding frequency; and (c) the estimated weight of food

TABLE 2. Correlations of male parental effort and female behavioral variables affecting confidence of paternity. Statistic is Pearson's correlation coefficient (n in parentheses).[a]

Female behavioral variables	Percent of feedings provisioned by male	Percent of food in weight provisioned by male	Percent of nest attendance by male
No. EPC attempts received by female prior to egg laying	0.14 (24)	0.05 (22)	0.02 (18)
No. EPC attempts received by female in her mate's presence	−0.11 (24)	0.27 (22)	0.25 (18)
Percent of arrivals upon which female received EPC attempt in her mate's absence	0.07 (17)	−0.15 (15)	0.08 (14)
No. EPCs accepted by female	0.02 (24)	0.09 (22)	0.19 (18)
No. times female was present in arena when her mate first arrived	0.12 (20)	−0.20 (18)	0.01 (15)
No. WPCs accepted by female	−0.01 (26)	−0.06 (24)	0.32 (21)
Percent of WPC attempts female accepted	−0.35 (25)	−0.33 (23)	0.40 (20)

[a] None of correlations significant at $P < 0.05$.

TABLE 3. Comparison of parental effort made by males whose mates did and did not accept an EPC in the mating arenas. Statistics refer to Mann-Whitney U-test.

Percentage of parental care provided by male	Cuckolded Mean ± SD (n)	Not cuckolded Mean ± SD (n)	z	P
Feedings	40.4 ± 7.5 (6)	44.8 ± 13.6 (18)	0.77	0.45
Food in weight	49.2 ± 8.9 (5)	48.6 ± 12.5 (17)	0	1.0
Overnight nest attendance	51.1 ± 13.4 (7)	47.6 ± 16.3 (11)	0.41	0.68

delivered. Males contributed approximately the same as their mates in all three measures. They attended the nest on 51% of nights (Table 1). Males delivered 45.0% ± SD of 12.7% ($n = 26$, range 24–68) of feedings and provided 49.3 ± 11.3% ($n = 24$, range 16–72) of food in weight. Despite parental effort being equal on average, there was marked variation in the proportion contributed by each sex in all three measures (e.g. with males providing from 16 to 72% of food in weight).

To test whether this variation in male effort was related to confidence of paternity, I correlated the three measures of parental effort with seven female behaviors that could affect the male's risk of being cuckolded. None of the correlations in Table 2 was significant and, while the confidence-of-paternity hypothesis predicted positive relationships, 7 of 21 (33%) correlations were negative. I also compared the parental effort of males whose mates did and did not obtain at least one EPC. Since 82% of EPCs were performed in the mating arenas (Wagner 1991a), use of arena EPCs in this analysis should be reasonably accurate in predicting whether females accepted EPCs prior to laying. There were no differences in any of the three measures of parental effort between the two classes of males (Table 3). Thus, I found no evidence that confidence of paternity affects male parental effort.

An alternative explanation for the observed variance in relative male effort could simply be that there is variation in male ability; males who demonstrate abilty, or "vigor" in certain activities may perform well generally (Møller 1988). To test the "male-quality hypothesis," I correlated the same three measures of male effort with seven activities that males performed in the mating arenas prior to egg laying that could be associated with vigor (Table 4). Only 3 (14%) of the 21 correlations were significant, and 8 (38%) of the correlations were of the sign opposite to that predicted. The percentage of fights won was correlated with the percentage of male feedings (Fig. 1), and arrival time was correlated with both measures of feeding. Arrival time is a measure of arena attendance, which may be a costly activity because it reduces foraging time. The negative correlations indicate that males who arrived in the arenas earlier in the morning (in the prelaying period) were those who subsequently delivered a higher proportion of food to the nestling. Another measure of arena attendance is the number of days the male was present. However, this measure was not correlated with paternal effort. The frequencies of three behaviors that were associated with male EPC success (male copulation interference, fights won, and EPC attempts; Wagner 1992a) also were not correlated with male effort, and neither was EPC success correlated with male effort. There

TABLE 4. Correlations of male parental effort and variables associated with male quality. Statistic is Pearson's correlation coefficient (n is in parentheses).

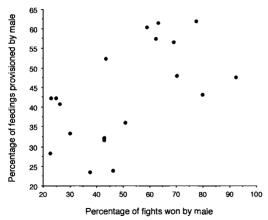| Male variables	Percent of feedings provisioned by male	Percent of food in weight provisioned by male	Percent of nest attendance by male
Percentage of fights won	0.53* (19)	0.19 (17)	0.26 (15)
No. fights won	0.11 (20)	0.09 (18)	0.08 (17)
No. successful EPCs	−0.29 (20)	0.30 (18)	−0.35 (17)
No. EPC attempts	0.08 (20)	−0.05 (18)	−0.27 (17)
No. copulations with which male interfered	−0.97 (20)	0.21 (18)	−0.37 (17)
Mean arrival time to mating arena	−0.45* (20)	−0.51* (18)	0.15 (16)
No. days male attended arena	0.08 (20)	−0.05 (18)	−0.27 (17)

* $P < 0.05$.

Fig. 1. Relationship between percentage of fights males won in mating arenas prior to nestling period and males' subsequent parental contribution in terms of percentage of feedings provisioned ($r = 0.53$, df = 18, $P < 0.02$; analysis of arcsine-transformed data).

was also no statistical association between male effort in overnight attendance and either of the two measures of feeding (percentage of feedings, $r = -0.05$, df = 18, $P = 0.84$; percentage of food in weight, $r = -0.21$, df = 16, $P = 0.23$).

DISCUSSION

The confidence-of-paternity hypothesis was not supported by data for Razorbills. Despite marked variation in female receptivity to EPCs and in relative male care, there was no evidence that males reduced their parental effort according to their mates' behavior toward other males, or the behavior of other males toward their mates. Burke et al. (1989) found in polyandrous Dunnocks (*Prunella modularis*) that beta males fed in proportion to their access to the female, but only Møller's (1988) study of Barn Swallows (*Hirundo rustica*) appears to support this hypothesis in a monogamous species, while three other studies have failed to find such relationships (Frederick 1987, Morton 1987, Westneat 1988).

The basis of the confidence-of-paternity hypothesis is that caring for unrelated offspring is necessarily detrimental. There may, however, be circumstances in which this is not true. For example, to explain cooperative breeding in birds, Zahavi (1976) offered the hypothesis that helpers can eventually become breeders by increasing their social status through the performance of costly behaviors.

In Arabian Babblers (*Turdoides squamiceps*), individuals in cooperative groups competed to feed young in order to increase their status, which could result in fitness benefits (Carlisle and Zahavi 1986). The breeding system of babblers allows for long-term interactions between individuals because babblers are nonmigratory and remain in the same territory among group members throughout the year (Zahavi 1974).

I propose that Zahavi's "status hypothesis" can be extended to migratory, nongroup breeding species that have high survivorship and maintain breeding sites (and therefore neighbors) between years. Razorbills are long lived (Hudson 1985) and breeding-site faithful (Harris and Birkhead 1985), and they even maintain consistent territories in the mating arenas within and between years (Wagner 1991a). Therefore, the potential exists for individuals to appraise each other over the long term. Given this potential, it is possible that various behaviors performed by a Razorbill in sight of other members of the colony may affect that individual's status. While there are behaviors that could affect male status, such as fighting ability or EPC success, it is also possible that males could gain or lose status by their performance as parents. Because advertisement should be costly to be honest (Zahavi 1975, 1977, Grafen 1990), the apparent costliness of provisioning offspring may provide a reliable index by which Razorbills could measure the quality of their neighbors. Social status would affect the male's fitness if it influences future prospects for pair bonding, EPCs, breeding sites, and the outcome of aggressive encounters with other males. Feeding an offspring of uncertain paternity also could be viewed as a form of courtship feeding, one year in advance, whereby the male attempts to convince his mate to re-pair with him in the following year, when his mate may increase his confidence of paternity.

The status hypothesis makes predictions that can be tested in a long-term study. It predicts that parental effort will have social consequences in the following year, specifically, that males or females who provide poorly will have a higher rate of divorce, and less success in obtaining future mates. If females use male parental effort as a criterion for selecting EPC partners, then a possible cost to males of provisioning poorly is reduced success in obtaining EPCs. Across species, the status hypothesis predicts that males in long-lived, breeding-site-

faithful species are less likely to reduce parental effort according to their confidence of paternity, compared with males in species that do not encounter their neighbors and mates from one year to the next.

In addition to losing fitness through lowered status by provisioning poorly, a male also could suffer if reduced effort decreased the survivorship of his mate by forcing her to over-work (Gowaty 1983); in the case of Razorbills, most individuals re-pair with their previous year's partner (Lloyd 1976; Wagner, unpubl. data). If the male Razorbill gains by preserving the viability of his partner, it could help explain why the male is the parent which escorts the fledgling to sea. Since the female has already expended more energy than the male by producing the large egg, and since the other parental duties are equally shared on average, one might expect the burden of escorting the fledgling to be borne by the male.

Another reason why male Razorbills would not necessarily reduce effort in response to their mates' receptivity to EPCs is that EPCs may be unlikely to result in fertilizations. This is suggested by the finding that females who accepted EPCs permitted their mates a higher percentage of WPC attempts than females who did not accept EPCs (Wagner 1992a). It is possible that females had sought EPCs not for fertilizations by extra-pair males, but for insurance against their mates' infertility (Wagner 1992a). If insurance is the aim of females, then males may in fact suffer very low risks of cuckoldry, which would be the case if the percentage of inseminations (2%) provided by EPCs is a predictor of fertilization frequency (Wagner 1991a).

In conclusion, while the confidence-of-paternity hypothesis predicts a reduction in male parental effort in response to female promiscuity, there are also reasons to expect that males will not reduce care. The status hypothesis provides a basis for investigating alternative predictions. Given the paucity of support for the confidence of paternity hypothesis, and theoretical alternatives to explain parental care by uncertain males, it may be fruitful to consider circumstances in which care giving to unrelated offspring can be beneficial.

LITERATURE CITED

BARRETT, R. T. 1984. Comparative notes on eggs, chick growth and fledging in the Razorbill *Alca torda* in north Norway. Seabird 7:55–61.

BIRKHEAD, T. R., L. ATKIN, AND A. P. MØLLER. 1987. Copulation behaviour of birds. Behaviour 101:101–138.

BURKE, T., N. B. DAVIES, M. W. BRUFORD, AND B. J. HATCHWELL. 1989. Parental care and mating behaviour of polyandrous Dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. Nature (Lond.) 338:249–251.

CARLISLE, T. R., AND A. ZAHAVI. 1986. Helping at the nest, allofeeding and social status in immature Arabian Babblers. Behav. Ecol. Sociobiol. 18:339–351.

CRAIG, J. L., AND I. G. JAMIESON. 1985. The relationship between presumed gamete contribution and parental investment in a communally breeding bird. Behav. Ecol. Sociobiol. 17:207–211.

CRAMP, S. (Ed.). 1985. The birds of the western Palearctic, vol. IV. Oxford Univ. Press, Oxford.

FREDERICK, P. 1987. Responses of male White Ibises to their mate's extra-pair copulations. Behav. Ecol. Sociobiol. 21:223–228.

GOWATY, P. A. 1983. Male parental care and apparent monogamy among Eastern Bluebirds (*Sialia sialis*). Am. Nat. 121:149–157.

GRAFEN, A. 1990. Biological signals as handicaps. J. Theor. Biol. 144:517–546.

HARRIS, M. P., AND J. R. G. HISLOP. 1978. The food of young Puffins *Fratercula arctica*. J. Zool. (Lond.) 185:213–236.

HARRIS, M. P., AND T. R. BIRKHEAD. 1985. Breeding ecology of the Atlantic Alcidae. Pages 155–204 *in* The Atlantic Alcidae (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, London.

HARRIS, M. P., AND S. WANLESS. 1986. The food of young Razorbills on the Isle of May and a comparison with that of young Guillemots and Puffins. Ornis. Scand. 17:41–46.

HUDSON, P. J. 1982. Nest site characteristics and breeding success in the Razorbill *Alca torda*. Ibis 124:355–359.

HUDSON, P. J. 1985. Population parameters for the Atlantic Alcidae. Pages 233–261 *in* The Atlantic Alcidae (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, London.

LLOYD, C. S. 1976. The breeding biology and survival of the Razorbill *Alca torda* L. D.Phil. thesis, Univ. Oxford, Oxford.

LLOYD, C. S. 1977. The ability of the Razorbill *Alca torda* to raise an additional chick to fledging. Ornis Scand. 8:155–159.

MARTIN, P. A., T. J. REIMERS, J. R. LODGE, AND P. J. DZUIK. 1974. The effect of ratios and numbers of spermatozoa mixed from two males on the proportion of offspring. J. Reprod. Fertil. 39:251–258.

MAYNARD SMITH, J. 1977. Parental investment: A prospective analysis. Anim. Behav. 25:1–9.

MCKINNEY, F., K. M. CHENG, AND D. J. BRUGGERS. 1984. Sperm competition in apparently monogamous birds. Pages 523–545 *in* Sperm competition and the evolution of animal mating systems (R. L. Smith, Ed.). Academic Press, New York.

MØLLER, A. P. 1988. Paternity and paternal care in the Swallow *Hirundo rustica*. Anim. Behav. 36:996–1005.

MORTON, E. S. 1987. Variation in mate guarding intensity by male Purple Martins. Behaviour 101:211–224.

MORTON, E. S., L. FORMAN, AND M. BRAUN. 1990. Extrapair fertilizations and the evolution of colonial breeding in Purple Martins. Auk 107:275–283.

ORING, L. W. 1982. Avian mating systems. Pages 1–92 *in* Avian biology, vol. 3 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, London.

PENNYCUICK, C. J. 1987. Flight of seabirds. Pages 43–63 *in* Seabirds: Feeding ecology and role in marine ecosystems (J. P. Croxall, Ed.). Cambridge Univ. Press, Cambridge.

SHERMAN, P. W., AND M. L. MORTON. 1988. Extrapair fertilizations in Mountain White-crowned Sparrows. Behav. Ecol. Sociobiol. 22:413–420.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136–179 *in* Sexual selection and the descent of man 1871–1971 (B. Campbell, Ed.). Aldine Press, Chicago.

WAGNER, R. H. 1991a. The role of extra-pair copulation in Razorbill mating strategies. D.Phil. thesis, Univ. Oxford, Oxford.

WAGNER, R. H. 1991b. Evidence that female Razorbills control extra-pair copulations. Behaviour 118:157–169.

WAGNER, R. H. 1991c. The use of extra-pair copulations for mate appraisal by Razorbills. Behav. Ecol. 2:198–203.

WAGNER, R. H. 1992a. The pursuit of extra-pair copulations by monogamous female Razorbills: How do females benefit? Behav. Ecol. Sociobiol. 29:455–464.

WAGNER, R. H. 1992b. Extra-pair copulations in a lek: The secondary mating strategy of monogamous Razorbills. Behav. Ecol. Sociobiol. In press.

WERREN, J. H., M. R. GROSS, AND R. SHINE. 1980. Paternity and the evolution of male parental care. J. Theor. Biol. 82:619–631.

WESTNEAT, D. F. 1988. Male parental care and extrapair copulations in the Indigo Bunting. Auk 105:149–160.

WESTNEAT, D. F. 1990. Genetic parentage in the Indigo Bunting: A study using DNA fingerprinting. Behav. Ecol. Sociobiol. 27:67–76.

WESTNEAT, D. F., P. W. SHERMAN, AND M. L. MORTON. 1990. The ecology and evolution of extra-pair copulations in birds. Curr. Ornithol. 7:331–369.

WITTENBERGER, J. F., AND R. L. TILSON. 1980. The evolution of monogamy: Hypotheses and evidence. Annu. Rev. Ecol. Syst. 11:197–232.

ZAHAVI, A. 1974. Communal nesting in the Arabian Babbler: A case of individual selection. Ibis 116:84–87.

ZAHAVI, A. 1975. Mate selection—A selection for a handicap. J. Theor. Biol. 53:205–214.

ZAHAVI, A. 1976. Cooperative nesting in Eurasian birds. Pages 685–693 *in* Proceedings 16th International Ornithological Congress (H. J. Frith and J. H. Calaby, Eds.). Canberra, 1974. Australian Academy of Science, Canberra.

ZAHAVI, A. 1977. The cost of honesty. (Further remarks on the handicap principle.) J. Theor. Biol. 67:603–605.