



Responses to Mate Loss by Herring Gulls *Larus argentatus* and Great Black-Backed Gulls *Larus marinus*

Author(s): Gregory J. Transue and Joanna Burger

Source: *Ornis Scandinavica*, Vol. 20, No. 1, (Mar., 1989), pp. 53-58

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

Stable URL: <http://www.jstor.org/stable/3676708>

Accessed: 11/04/2008 17:38

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=black>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We enable the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

Responses to mate loss by Herring Gulls *Larus argentatus* and Great Black-backed Gulls *Larus marinus*

Greggory J. Transue and Joanna Burger

Transue, G. J. and Burger, J. 1989. Responses to mate loss by Herring Gulls *Larus argentatus* and Great Black-backed Gulls *Larus marinus*. – *Ornis Scand.* 20: 53–58.

Herring Gulls and Great Black-backed Gulls were used to examine the reactions of individuals to mate loss. Late in incubation, one member of each of 41 incubating pairs was experimentally removed and its mate's response observed. We predicted that deserted individuals unable to obtain a replacement mate, would also desert the reproductive attempt, and that there would be no sexual difference in responses.

All individuals either abandoned the initial clutch or brood. Only one individual replaced a lost mate that season. Males, however, abandoned their eggs significantly earlier than did females. There was no significant difference in the responses of the two species, nor any significant species-sex interaction.

We review and suggest a number of possible explanations for why males and females should react differently. These include cumulative reproductive effort, the tertiary sex ratio, the physical reserves of the deserted mate, the possibility and consequences of mixed reproductive strategies, and potential differences in replacement costs between the sexes due to differences in what each sex regards as its primary asset.

G. J. Transue and J. Burger, Dept of Biological Sciences, Rutgers University, Piscataway, NJ 08854, USA.

Introduction

In monogamous organisms, mate loss through death, injury, or deliberate desertion can have a dramatic effect on an individual's reproductive success. Studies and theoretical discussions of desertion and mate loss have examined the cause of desertion, the decision to desert, the replacement of the deserter, and the response of the deserted mate (e.g. Trivers 1972, Dawkins and Carlisle 1976, Maynard Smith 1977, Grafen and Sibley 1978, Ridley 1978, Pienkowski and Greenwood 1979, Beissinger 1987). We examined the reactions of individuals to mate loss late in the incubation period in two long-lived, monogamous species of seabirds, the Herring Gull *Larus argentatus* and the Great Black-backed Gull *Larus marinus*. By experimentally removing one mate from incubating pairs, we could observe the individual re-

sponses to mate loss and detect any sexual differences in the responses.

Once desertion or mate loss has occurred, a deserted individual can do one of three things (Trivers 1972): (1) abandon the reproductive attempt, (2) continue the attempt unaided, or (3) replace the lost mate. Seabirds are generally unable to rear offspring alone (Lack 1968, van Rhijn and Groothuis 1985), often due to predation on eggs and offspring. Documented instances of successful rearing by single parent seabirds are rare (Nisbet et al. 1978). Conover's (1984a) observations on deserted Ring-billed Gulls *Larus delawarensis* and California Gulls *Larus californicus* indicated that single gulls are unable to rear chicks by themselves. Consequently, we predicted that the deserted gulls would either abandon the reproductive attempt or replace the lost mate.

Received 22 February 1988

Revised 4 October 1988

Accepted 4 October 1988

© ORNIS SCANDINAVICA

Table 1. Time until abandonment by both species following removal of mate.

Species	Sex	N	Mean \pm SD (d)	Range (d)
Great Black-backed Gull	F	5	3.0 \pm 1.2	1 – 4
	M	17	2.6 \pm 1.5	1 – 7
Herring Gull	F	9	5.6 \pm 3.2	1 – 10
	M	9	2.7 \pm 1.8	1 – 5
Both species combined ^a	F	14	4.6 \pm 2.9	1 – 10
	M	26	2.6 \pm 1.6	1 – 7

^aANOVA = $p < 0.03$

Secondly, we expected that there would be no difference in responses between the sexes. We felt there is sufficient evidence suggesting that by the end of incubation, both sexes have invested equally in the reproductive attempt (Gladstone 1979, Butler and Janes-Butler 1983, Burger 1984, 1987). Thus when deserted through our treatment, individuals of both sexes would have equal replacement costs and therefore would respond similarly.

Methods

The experiment was conducted on Wooden Ball Island, Knox County, Maine (43°51'N 68°49'W) during May and June of 1983 and 1984. Wooden Ball, a 55 ha granitic island, approximately 32 km from the mainland, is part of the Matinicus group of islands discussed by Drury (1973). The island, covered in the spring by a less than 10 cm high grass-chickweed *Cerastium arvense* turf with cranberry *Vaccinium macrocarpon* bogs and bay-berry *Myrica pensylvanica* thickets interspersed, supported about 250 pairs of Herring Gulls and 90 pairs of Great Black-backed Gulls in 1983 and 1984.

Gulls were marked by dye-soaked sponges when they sat to incubate and thus could be identified as breeders at particular nest sites. Only nests on the southern third of the island were used. Once the adults were marked, treadle traps were used to trap one adult from each of 41 nests. Each year, all trapping was completed within one week. Previous use of treadle traps by Burger had not caused abandonment and was therefore not considered to affect the subsequent behavior of the resident.

Trapping was done late in the incubation period, the first week in June in 1983 (9 Great Black-backed Gulls) and the last week in May and the first week in June in 1984 (14 Great Black-backed Gulls and 18 Herring Gulls). Hatching began on 8 June in 1983 and 11 June in 1984. Only adults with complete (3 eggs) clutches were trapped. Nests under rock overhangs or on the seaward cliffs were not used; otherwise, nests were chosen at random. Collected birds were sexed by dissection.

Once birds were removed, the nests were observed from blinds for at least three hours every other day.

Nest sites were checked daily to determine nest contents and condition. Nests were observed until 30 June in 1983 and 16 June in 1984. The 32 nests in 1984 were checked again on 21 July. The 1983 nests were checked periodically through August. Data recorded included the behavior of deserted individuals, conditions of the nest, and time until egg disappearance. As a control for disturbance, 33 non-experimental nests in the same area were routinely checked along with the experimental nests. The data were analyzed using SAS (Statistical Analysis System 1982).

Results

All 41 deserted individuals either failed to hatch their eggs ($n=40$) or fledge their chicks ($n=1$) (Tab. 1). Only one individual (a female Herring Gull) eventually replaced its lost mate and clutch that same year. All deserted individuals continued incubation and nest site defense until eggs disappeared. Partial loss of clutches was not observed. We never saw eggs being taken, but as two clutches lasted 10 days, the gulls were able to protect their eggs for several days. No obvious courtship behaviors (head tossing, adoption of flat posture by females) were observed and once the eggs were gone, ninety-three percent (93%) of the deserted individuals ($n=37$) were never seen at the nest site again. Three gulls (7%) were seen for less than one minute the day following egg loss, but were never seen at the nest site thereafter. New prospectors were not evident on the empty territories.

Of the 33 control nests routinely checked, only two (6%) were either abandoned or preyed upon during the three weeks of nest checks. Control birds performed normal behaviors, such as incubation and territorial defense at nest sites which were closer to the blinds than the nest sites of experimental birds.

There was a statistically significant difference between the two sexes in terms of the time until egg disappearance (ANOVA, $F=5.42$, $p < 0.03$, Tab. 1), with male attempts of both species ending more quickly than did female attempts. As the difference between the responses of the two species and the species-sex interac-

tion in the ANOVA were insignificant, the responses of the two species will be discussed as one.

One male Great Black-backed Gull was excluded from the ANOVA just discussed because during the night after his mate was removed, two of his three eggs hatched. One chick was found dead at the nest site five days later, while the other chick survived for ten days. The male had attended the chicks during each observation period until the chicks were gone. After that time, the site was never attended. This individual was not included in the statistical analysis because it was presented with a different expected benefit/expected cost calculation from that of all others.

The female Herring Gull who replaced her lost mate had a newly hatched chick and one egg on 21 July 1984. Her mate had been removed on 10 June, her eggs were gone the following day, and she laid her replacement clutch on 21 or 22 June. This two week replacement period is similar to that reported by Goethe (1937) and Salomonson (1939).

Discussion

The loss of eggs and chicks by deserted gulls was undoubtedly the result of either a temporary or a permanent abandonment of the nest site. In either case, the individual knowingly left the nest unprotected, thus both actions could be considered abandonment. As predation is unlikely while a parent is attending the nest, egg loss probably occurred after abandonment by the remaining parent. The interesting question is why reproductive attempts of males ended sooner than those of females.

Earlier male abandonment could be explained through the assumption that, by the onset of incubation, females have invested more in offspring due to greater gamete cost and that reproductive strategies of males and females are based on this difference. Females should try longer to obtain aid because of the larger replacement cost of ova relative to sperm. Although numerous theories have included this assumption, (e.g. Trivers 1972, Alcock 1975, Wilson 1975, Dawkins 1976, Pierotti 1981), it seems erroneous because other types of reproductive investment are not considered and the importance of the disparity between sperm and ovum cost may be over-emphasized (Gladstone 1979, Drewsbury 1982).

We used Low's (1978) reproductive effort model because it includes mating effort. Female gulls may have exerted more parental effort through the incubation period due to gamete cost, but males have probably exerted more mating effort through mate acquisition, territory acquisition and defense (Montevocchi and Porter 1980, Pierotti 1981, Burger 1984, Morris 1987), courtship feedings (Nisbet 1973), and mate guarding (Mock 1979). For these gulls and similar species, cumulative reproductive effort may be approximately equal by the end of incubation (Gladstone 1979).

A few studies support the assumption of equal reproductive effort by the end of incubation. Both Butler and Janes-Butler (1983) working with Great Black-backed Gulls and Burger (1984, 1987) working with Herring Gulls have stated that reproductive effort of males and females is equal by the end of incubation. Therefore because other types of investments are not considered and because there is evidence indicating equal reproductive effort by the end of incubation, we feel that an explanation based on gamete cost is doubtful and that one or more of the following explanations is likely to explain the results.

Differential abandonment by the sexes could be the result of a biased tertiary sex ratio. If the tertiary sex ratio is biased in favor of females as it is in other gull populations (Mills 1973, Hunt et al. 1980, Shugart 1980, Burger and Gochfeld 1981, Conover 1984b, Conover and Hunt 1984a,b), males would have no problems in obtaining mates, while some females would need to wait for a monogamous relationship (Murray 1984). Offspring could be more valuable to a female than to her mate because she may have difficulty obtaining mates. Supernormal clutches have been used as indicators of biased sex ratios (Hunt and Hunt 1977, Conover et al. 1979, Ryder and Somppi 1979, Hunt et al. 1980, Conover and Hunt 1984a, b). But, as there have been no supernormal clutches on Wooden Ball in three years of observation, the tertiary sex ratio is probably not skewed.

Males may also desert more quickly if they exert more reproductive effort than females by the end of incubation; therefore, they may be more physically exhausted than females. Male gulls are usually found to be more aggressive and more likely to be involved in an aggressive encounter prior to chick hatching than are females (Tinbergen 1960, Burger and Beer 1975, Pierotti 1981, Southern 1981, Morris and Bidochka 1982, Butler and Janes-Butler 1983, Burger 1984, 1987). Male gulls also provide courtship feedings (Brown 1967, Niebur 1981, Pierotti 1981, Tasker and Mills 1981, Burger 1987). These activities may cause males to have lower energy reserves than their mates thereby making them more likely to temporarily abandon the nest site to feed. While the nest site is unattended, egg loss may occur as a result of predation. The earlier abandonment by males may be a result of their physical conditions, rather than from considerations of the reproductive value of offspring.

If the two sexes differ in their potential to survive until the next breeding season, the sex less likely to survive would be expected to try longer as it would have a lower future reproductive potential. Available data on differential survivorship of the sexes in gulls suggests that females have greater per annum survivorship rates than do males; therefore, females would have greater future reproductive potentials than males. Although Chabryzk and Coulson (1976) found little evidence for differential survivorship of the sexes in Herring Gulls,

Coulson and Butterfield (1986) found that female Herring Gulls had half the annual mortality rate of males. Similarly, Coulson and Wooller (1976) and Coulson and Thomas (1985) found that female Black-legged Kittiwakes *Rissa tridactyla* had higher survivorship rates than did males. Thus, the responses of the gulls in this study are counter to what available survivorship data would suggest.

Another explanation suggested by our results is that females may normally be alone more on the territory and may take longer to realize that the male is not going to return than it takes for a male to realize a female is not going to return. However, data from other gull studies do not support this explanation. Tinbergen (1960) reported that incubation bouts in Herring Gulls were generally divided equally between the sexes. Other studies of gull incubation have found that, in general, male and female gulls spend approximately the same amounts of time incubating (Beer 1961, Burger and Beer 1975, Pierotti 1981, Burger 1984, 1987). Pierotti (1981) did find that in two populations, female Western Gulls *Larus occidentalis* incubated more than did males, but Ytreberg (cited in Beer 1961) found that male Black-headed Gulls *Larus ridibundus* incubated more than did females.

Except for two populations of Western Gulls observed by Pierotti (1981), male gulls have been found to spend at least as much time on the territory as do females and in some cases more (Vermeer 1963, Morris and Black 1980, Pierotti 1981, Burger 1984, 1987). However, the total amount of time an individual spends on the territory does not necessarily indicate that the lengths of time each sex spends away from the nest site are equal. If the sexes spend different lengths of time away from the nest site, perhaps one sex would be able to detect the absence of a mate more quickly.

Unfortunately, few data exist on the length of bouts for each sex on or away from the nest site. Tinbergen (1960) stated that Herring Gull incubation bouts were regular and ranged between two and five hours in length. Inferential data suggest however, that females may be away from the nest site more than males. When in the incubation period, Herring Gulls continuously protect the nest site through incubation (Tinbergen 1960, Burger 1987). If each sex incubates approximately half the time as discussed earlier, then incubation bout length must on average be the same for each sex. Even if bout length varies through the day, neither sex could be away from the nest more than the other and still do half the incubation. Consequently, the only relevant differences in time away from the nest site would be in the time each sex spends on the territory while not incubating.

Burger (1984, 1987) found that in Herring Gulls, the amount of time spent on territory when not incubating was approximately equal between the sexes; again suggesting that females should be able to realize the disappearance of mates at least as soon as can males. Yet,

females in our study continued the reproductive attempt longer. Thus, neither the time present on the territory or spent incubating nor the length of attendance periods appear to provide a reasonable explanation for earlier male abandonment.

The mechanics of internal fertilization and the resulting initial internalization of the zygote also provide a possible explanation for earlier male abandonment. Males may be able to use extra-pair copulations to increase their reproductive success (Trivers 1972, Mock 1979, Power 1980, Pierotti 1981, Fitch and Shugart 1984). Females can only use extra-pair copulations to produce better quality offspring by mating with males they see as being superior to their mates (Borgia 1979, Gladstone 1979, Buitron 1983), but not to increase their immediate reproductive success. If there is a possibility that a male has been cuckolded, he may be more likely to end the reproductive attempt. Conversely, if males are able to cuckold others, they would have a greater reproductive success than females and therefore may be more likely to end the attempt because each offspring has less reproductive value to the male than to the female. If a female has quality offspring, she may be more likely to continue the attempt in hopes of attaining aid.

Hunt and Hunt (1977), Conover et al. (1977), and Ryder and Somppi (1979) have documented female-female pairs with fertile eggs, suggesting extra-pair copulations in gulls. Other studies have documented attempts at extra-pair copulations in gulls (Burger and Beer 1975, Pierotti 1981, Morris and Bidochka 1982, Fitch and Shugart 1984). Although Fitch (1983) argued that extra-pair copulations are not adaptive in Herring Gulls, extra-pair copulations may occasionally result in viable offspring.

A final possible explanation is that males and females may have different replacement costs because, in an ultimate sense, they may differ in what they regard to be the more important asset to be replaced. Prior to hatching, males have primarily invested in territory and mate acquisition, while females have invested mainly in the eggs. After a mate is lost, individuals are left with a territory and the eggs. Males may regard the territory, his primary contribution to the reproductive attempt up until hatching, as being the most important item to be replaced, rather than the eggs, the primary contributions of the female. Replacement of the territory may be less costly for the male than replacement of the eggs is for the female because he is already established at that territory and may not need to re-acquire the territory the next season, but only re-assert himself. The fact that two pairs of wing-tagged Great Black-backed Gulls on another part of the island were able to retain their territories the following year, despite abandoning their nest sites after nest failure early in the incubation stage, supports this possibility. The female though, must completely start over by producing new eggs. To test what each sex regards as the more important asset to replace

would be very difficult because of the spacial inter-relationship between the territory, the nest, and the eggs.

This experiment has shown that late in incubation when replacement mates were not obtained, Herring Gulls and Great Black-backed Gulls abandoned the reproductive attempt, but that males of both species did so more quickly than did females. This result indicates that models which try to make accurate predictions about desertion may need to consider the tertiary sex ratio (Murray 1984), the possibility and consequences of mixed reproductive strategies (Trivers 1972), and possible differences in replacement costs as they all potentially affect reproductive success. A similar experiment conducted earlier in the breeding cycle may result in different results as replacement mates may prove to be available. Thus the stage in the breeding cycle the pair is in is also an important parameter to be included in any model. Models which attempt to predict when an individual would benefit from deserting also need to consider the parameters we have discussed.

Acknowledgements – We thank B. G. Murray, Jr., C. Leck, and M. Gochfeld for their critical reviews of the manuscript. M. Conover also provided helpful comments. Financial support was provided by the Frank M. Chapman Memorial Fund of the American Museum of Natural History, the Anne B. & James H. Leathem Scholarship Fund of the Department of Biological Sciences of Rutgers University, and a Grant-in-Aid of Research from Sigma Xi, The Scientific Research Society. Logistical and material support was provided by the Fratercula Fund of the National Audubon Society through Dr. Stephen Kress, and we gratefully acknowledge his help and support throughout the study.

We thank Thomas Watkinson for granting permission to work on Wooden Ball and Ronald Watkinson for logistical aid. Special thanks go to Doug Fraher, Beth Panzini, Steve Pleasant, and Brett Transue for their field assistance. Very special thanks go to Mary Ruth Peters for her understanding and support throughout the study.

References

- Alcock J. 1975. Animal behavior: An evolutionary approach. – Sinauer, Sunderland, Mass.
- Beer, C. G. 1961. Incubation and nest-building behaviour of black-headed gulls. I. Incubation behaviour in the incubation period. – Behaviour 18: 62–106.
- Beissinger, S. R. 1987. Anisogamy overcome: female strategies in Snail Kites. – Am. Nat. 129: 486–500.
- Borgia, G. 1979. Sexual selection and the evolution of mating systems. – In: Blum, M. and Blum, N. (eds). Sexual selection and reproductive competition in insects. – Academic Press, New York, pp 19–80.
- Brown, R. G. B. 1967. Courtship behaviour in the Lesser Black-backed Gull. – Behaviour 29: 122–153.
- Buitron, D. 1983. Extra-pair courtship in black-billed magpies. – Anim. Behav. 31: 211–220.
- Burger, J. 1984. Pattern, mechanism and adaptive significance of territoriality in Herring Gulls (*Larus argentatus*). – Ornith. Monogr. No. 34, American Ornithologists Union, Washington, D. C.
- 1987. Selection for equitability in some aspects of reproductive investment in Herring Gulls *Larus argentatus*. – Ornith. Scand. 18: 17–23.
- and Beer, C. 1975. Territoriality in the Laughing Gull (*Larus atricilla*). – Behaviour 55: 301–320.
- and Gochfeld, M. 1981. Unequal sex ratios and their consequences in Herring Gulls (*Larus argentatus*). – Behav. Ecol. Sociobiol. 8: 125–28.
- Butler, R. G. and Janes-Butler, S. 1983. Sexual differences in the behavior of adult Great Black-backed Gulls (*Larus marinus*) during the pre- and post-hatch periods. – Auk 100: 63–75.
- Chabryk, G. and Coulson, J. C. 1976. Survival and recruitment in the Herring Gull *Larus argentatus*. – J. Anim. Ecol. 45: 187–203.
- Conover, M. R. 1984a. Consequences of mate loss to incubating Ring-billed and California Gulls. – Wilson Bull. 96: 714–716.
- 1984b. Occurrence of supernormal clutches in the Laridae. – Wilson Bull. 96: 249–267.
- and Hunt, G. L., Jr. 1984a. Experimental evidence that female-female pairs in gulls result from a shortage of breeding males. – Condor 86: 472–476.
- and Hunt, G. L., Jr. 1984b. Female-female pairing and sex ratios in gulls: an historical perspective. – Wilson Bull. 96: 619–625.
- , Miller, D. E., and Hunt, G. L., Jr. 1979. Female-female pairs and other unusual reproductive associations in Ring-billed and California Gulls. – Auk 96: 6–9.
- Coulson, J. C. and Butterfield, J. 1986. Studies on a colony of colour-ringed Herring Gulls *Larus argentatus*: I. Adult survival rates. – Bird Study 33: 51–54.
- and Thomas C. 1985. Changes in the biology of the Kittiwake *Rissa tridactyla*: a 31 yr study of a breeding colony. – J. Anim. Ecol. 54: 9–26.
- and Wooller, R. D. 1976. Differential mortality in breeding Kittiwake Gulls *Rissa tridactyla*. – J. Animal Ecol. 45: 205–213.
- Dawkins, R. 1976. The selfish gene. – Oxford University Press.
- and Carlisle, T. R. 1976. Parental investment: a fallacy. – Nature, Lond. 262: 131–133.
- Drewsbury, D. A. 1982. Ejaculation cost and male choice. – Am. Nat. 119: 601–610.
- Drury, W. H. 1973. Population changes in New England seabirds. – Bird-Banding 44: 267–313, 45: 1–92.
- Fitch, M. 1983. The evolutionary significance of the pair bond in a long-lived monogamous avian species; the Herring Gull. – Unpublished Ph.D. dissertation, Rutgers University.
- and Shugart, G. 1984. Requirements for a mixed reproductive strategy in avian species. – Am. Nat. 124: 116–126.
- Gladstone, D. E. 1979. Promiscuity in monogamous colonial birds. – Am. Nat. 114: 545–557.
- Goethe, F. 1937. Beobachtungen und Untersuchungen zur Biologie der Silbermöwe (*Larus argentatus* Pontopp) auf der Vogelinsel Memmert. – J. Orn. 85: 1–119.
- Grafen, A. and Sibley, R. 1978. A model of mate desertion. – Anim. Behav. 25: 645–652.
- Hunt, G. L., Jr. and Hunt, M. W. 1977. Female-female pairing in Western Gulls (*Larus occidentalis*) in southern California. – Science 196: 1466–1467.
- , Wingfield, J. C., Newman, A., and Farner, D. S. 1980. Sex ratio of Western Gulls on Santa Barbara Island, California. – Auk 97: 473–479.
- Lack, D. 1968. Ecological adaptations for breeding in birds. – Methuen, London.
- Low, B. 1978. Environmental uncertainty and the parental strategies of marsupials and placentals. – Am. Nat. 112: 197–213.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. – Anim. Behav. 25: 1–9.
- Mills, J. A. 1973. The influence of age and pair bonding on the breeding biology of the Red-billed Gull (*Larus novaehollandiae*). – J. Anim. Ecol. 42: 147–162.
- Mock, D. W. 1979. Display repertoire shifts and “extra-marital” courtship in herons. – Behaviour 69: 57–71.
- Montevocchi, W. and Porter, J. 1980. Parental care and related

- behavior before fledging in northern gannets (*Morus bassanus*) with reference to other marine birds. – In: Burger, J., Olla, B. and Winn, H. (eds). Behavior of marine animals. Vol. IV. Marine birds. Plenum, New York, pp. 323–366.
- Morris, R. D. 1987. Time partitioning of clutch and brood care activities in Herring Gulls: a measure of parental quality? – Studies in Avian Biology 10: 68–74.
- and Bidochka, M. J. 1982. Mate guarding in Herring Gulls. – Colonial Waterbirds 5: 124–129.
- and Black, J. E. 1980. Radio telemetry and Herring Gull foraging patterns. – J. Field Ornithol. 51: 110–118.
- Murray, Jr., B. G. 1984. A demographic theory on the evolution of mating systems as exemplified by birds. – In: Hecht, M. K., Wallace, B. and Prance, G. T. (eds). Evolutionary biology, Vol. 18. Plenum, New York, pp. 71–140.
- Niebur, V. 1981. An investigation of courtship feeding in Herring Gulls *Larus argentatus*. – Ibis 123: 218–223.
- Nisbet, I. C. T. 1973. Courtship-feeding, egg-size, and breeding success in common terns. – Science 241: 141–142.
- , Wilson, K. J. and Broad, W. A. 1978. Common Terns raise young after death of their mates. – Condor 80:106–109.
- Pienkowski, M. W. and Greenwood, J. S. 1979. Why change mates? – Biol. J. Linn. Soc. 12: 85–94.
- Pierotti, R. 1981. Male and female parental roles in the Western Gull under different environmental conditions. – Auk 98: 532–549.
- Power, H. 1980. Experiments on cuckoldry in the Mountain Bluebird. – Am. Nat. 116: 705–709.
- Ridley, M. 1978. Parental care. – Anim. Behav. 26: 904–932.
- Ryder, J. P. and Somppi, P. L. 1979. Female-female pairings in ring-billed gulls. – Auk 96: 1–5.
- Salomonson, F. 1939. Oological studies in Gulls. I. Egg producing power of *Larus argentatus* Pont. – Dansk Ornithol. Foren. Tidsskr. 33: 113–133.
- SAS User's Guide: Statistics. 1982. Ray, A. A. (ed.). SAS Institute Inc., Cary.
- Shugart, G. 1980. The frequency and distribution of polygyny in Great Lakes Herring Gulls in 1978. – Condor 82: 426–429.
- Southern, L. K. 1981. Sex-related differences in territorial aggression in Ring-billed Gulls. – Auk 98: 179–181.
- Tasker C. R. and Mills, J. A. 1981. A functional analysis of courtship feeding in the Red-billed Gull *Larus novaehollandiae scopulinus*. – Behaviour 77: 221–241.
- Tinbergen, N. 1960. The Herring Gull's World. – Basic Books, Inc., New York.
- Trivers, R. 1972. Parental investment and sexual selection. – In: Campbell, B. (ed.). Sexual selection and the descent of Man. Aldine, Chicago, pp. 136–179.
- Van Rhijn, J. and Groothuis, T. 1985. Biparental care and the basis for alternative bond-types among gulls, with special reference to Black-headed Gulls. – Ardea 73: 159–174.
- Vermeer, K. 1963. The breeding ecology of the Glaucous-winged Gull *Larus glaucescens* on Mandarte Island, B. C. – Occ. Pap. Br. Col. Prov. Mus. 13: 1–104.
- Wilson, E. O. 1975. Sociobiology. – The Belknap Press of Harvard University Press, Cambridge.
- Ytreberg, N. 1956. Contribution to the breeding biology of the Black-headed Gull *Larus ridibundus* in Norway. – Nytt Magasin for Zoologi 4: 5–106.