SPACING PATTERNS, MATING SYSTEMS, AND WINTER PHILOPATRY IN HARLEQUIN DUCKS

GREGORY J. ROBERTSON,[1,3] FRED COOKE,[1] R. IAN GOUDIE,[2,4] AND W. SEAN BOYD[2]

[1]*Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada; and*
[2]*Pacific Wildlife Research Centre, Canadian Wildlife Service, RR # 1, 5421 Robertson Road, Delta, British Columbia V4K 3N2, Canada*

ABSTRACT.—Many species of waterfowl form pair bonds during the nonbreeding season, yet current descriptions of mating systems and patterns of philopatry in waterfowl focus on the breeding grounds. We studied wintering Harlequin Ducks (*Histrionicus histrionicus*) in southwestern British Columbia to examine mating systems and philopatric behavior outside of the breeding season. The number of males at our study area was far more variable than that of females. Males that were unsuccessful in obtaining a mate were observed over a larger area than were paired males. Habitat use overlapped considerably among paired males, and no territorial boundaries were formed. Annual return rates to the nonbreeding grounds were high for both sexes (62% for females, 77% for males). Individuals not only returned to the general study area, but also to specific sections within the study area. Males that did not pair in the previous year returned to the study area in the subsequent year with the same frequency as males that had obtained mates; however, they tended to leave the study area prior to courtship. Therefore, it is possible that males return to the same wintering grounds each year to reunite with a previous mate. High levels of philopatry by both sexes allow pairs to reunite in fall, potentially increasing the benefits of philopatry for both sexes. *Received 19 January 1999, accepted 4 July 1999.*

THE RELATIONSHIP between mating systems and sex-biased dispersal in birds was first highlighted by Greenwood (1980). In species that exhibit mating systems based on resource defense (Emlen and Oring 1977), males tend to return to previous breeding areas at higher frequencies than do females. Males that return to the same site are able to use their prior knowledge of the local area to their advantage, whereas females are free to search for males of the highest quality. This situation is typified by most birds (Greenwood and Harvey 1982, Clarke et al. 1997). In contrast, in mating systems based on mate defense, females tend to return to (or remain at) the same areas with a higher frequency. Females in these systems are free to stay at preferred locations while males roam to find potential mates. Mammals tend to exhibit this pattern of female-biased philopatry (Greenwood 1980, Johnson and Gaines 1990).

Unlike most birds, waterfowl exhibit female-biased natal and breeding philopatry (Greenwood and Harvey 1982, Anderson et al. 1992) and a mate-defense mating system (McKinney 1986, Oring and Sayler 1992). This pattern is similar to that observed in mammals and is consistent with Greenwood's (1980) hypothesis.

Pairing in most species of migratory ducks occurs during the nonbreeding season before arrival at the breeding grounds (Rohwer and Anderson 1988); however, very little information exists on spacing patterns and behavior at the time of pair formation. Breeding waterfowl exhibit a wide range of spacing behavior, with some showing no evidence of territorial behavior and others being highly territorial (Anderson and Titman 1992). Presumably, wintering waterfowl could show any pattern within the range of spacing behavior and aggression that is seen during the breeding season (e.g. Savard 1988). Territorial behavior in other bird species is not restricted to the breeding grounds (e.g. Myers et al. 1979, Rappole and Warner 1980, Turpie 1995).

We studied spacing patterns and site fidelity in wintering Harlequin Ducks (*Histrionicus histrionicus*). Harlequin Ducks are small sea ducks that winter along coastal intertidal habitats

(Goudie and Ankney 1986) and are known to be philopatric to their nonbreeding grounds (Breault and Savard 1999). The main objectives of our study were twofold. The first was to broadly classify the Harlequin Duck's mating system as either resource defense or mate defense. This was achieved by studying movement patterns of males and females during the nonbreeding season and combining this information with behavioral data from other studies (Cooke et al. 1997, Gowans et al. 1997). We examined the stability of the number of males in the population and movements of individual males to determine whether males shared sections of habitat and whether they partitioned habitat into territories. The second objective was to explore which aspects of the mating system could explain any sex-biased philopatry of Harlequin Ducks to their wintering grounds. We examined philopatric behavior of previously paired and unpaired males to see whether specific sexual-selection pressures were related to the philopatric behavior of individuals.

METHODS

Study area and methods.—Our study was conducted from July 1994 to May 1997 in coastal southwestern British Columbia. The study site was composed of a 5.5-km stretch of rocky shoreline bounded by mud flats that were not used by Harlequins and thus effectively delimited the study area. Large boulders were scattered across the entire study site. Continuous access to the site was provided by a railway line on a dike (2 to 4 m high) that was marked every 160 m.

In the late summer and fall of each year, we captured and banded flightless individuals during the molting period. Researchers in sea kayaks rounded up the ducks and corralled them into a drive trap placed on an intertidal bench. Age and sex of after-hatching-year birds were determined by cloacal examination (hatching-year birds were not caught in our sample). Birds that possessed a bursa of Fabricius were classified as young birds in their second or third calendar year (Peterson and Ellarson 1978). Each bird was marked with a standard U.S. Fish and Wildlife Service metal band and a plastic band engraved with a unique two-character alphanumeric code. We captured 43 males and 29 females in 1994, 8 males and 18 females in 1995, and 12 males and 12 females in 1996.

We conducted weekly surveys and recorded numbers, sex, pairing status, and location of the sighting (to the nearest 160 m) of each Harlequin Duck. Pairs were identified by synchronous behaviors and mate guarding by males (Gowans et al. 1997). Ducks frequently hauled out onto rocks to rest and preen, and we read as many tarsal bands as possible during each survey.

Males began to arrive at the study area in June and July and immediately began the prebasic molt (Robertson et al. 1997). They were flightless during August and finished the prealternate molt by the end of September. Females began to arrive in August and early September and were flightless during September (Robertson et al. 1997). Pair formation began in October, and most females were paired by December (Gowans et al. 1997, Robertson et al. 1998).

Statistical analyses.—To assess the movements of individuals during the nonbreeding season, we needed a metric of site tenacity. Complex home-range estimators seemed unnecessary because our study area was linear. We used the variance in the mean distance among sighting locations as a metric of within-site movements (Robertson et al. 1999). The variance in sighting location was not correlated with the number of observations of each individual ($r = -0.066$ to 0.217, all $P > 0.1$). Parametric comparisons (t-tests) were used to compare the distribution of variances among groups because we wished to test for a difference between means and not for a difference between distributions (Stewart-Oaten 1995). The repeatability of mean sighting location between years was calculated from equations in Lessells and Boag (1987). To assess changes in the number of males and females at the study site, a cubic-spline smoothing function was fitted to the data. The residual variation from this function was used as an index of the magnitude of survey-to-survey changes in numbers of individuals. We used an α of 0.05 throughout, and all tests were two-tailed.

Return rates are percentages of marked birds that returned the next year. The probability of detecting an individual at least once during the year was very close to 1.00 (Robertson et al. 1999) owing to the high frequency of visits to the study area and the regularity with which we read the bands of birds that hauled out onto rocks. We calculated the probability of detecting individuals that were present in the study area from the ratio of the number of birds identified in each survey to the number of birds present at the study site. Therefore, these return rates are true return rates that are confounded only slightly by the probability of detecting individuals (Pollock et al. 1990, Lebreton et al. 1992). Because many of the marked birds were banded in the first year, some of the same individuals were present in all three years. Therefore, the tests we present for each of the three years should not be considered independent, but rather should be viewed as a confirmation that patterns hold across years (i.e. temporal replicates).
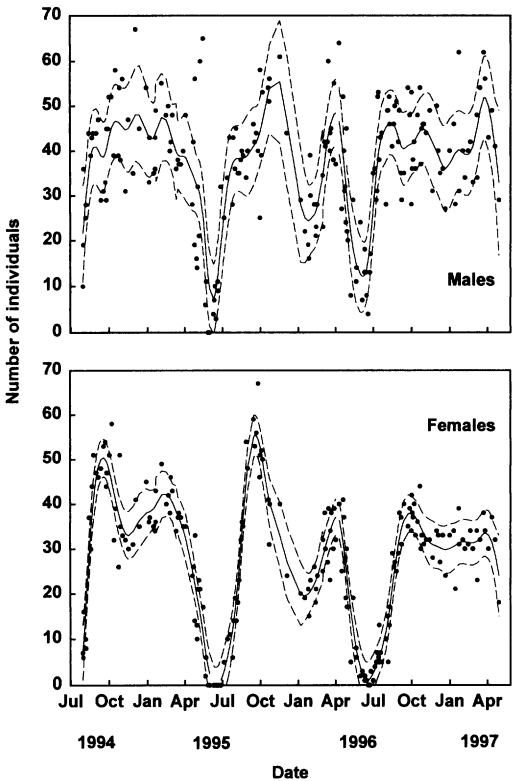
FIG. 1. Number of male and female Harlequin Ducks present at White Rock, British Columbia. Lines represent cubic smoothing splines and associated 95% confidence intervals.

RESULTS

Population structure.—The number of males present at the study site was more variable across survey dates than was the number of females (F-ratio of mean squared residuals from cubic spline, $F = 3.11$, df = 172.9 and 175.3, $P < 0.0001$; Fig. 1). The number of females peaked in September, possibly representing females that molted at the study area and then depart-
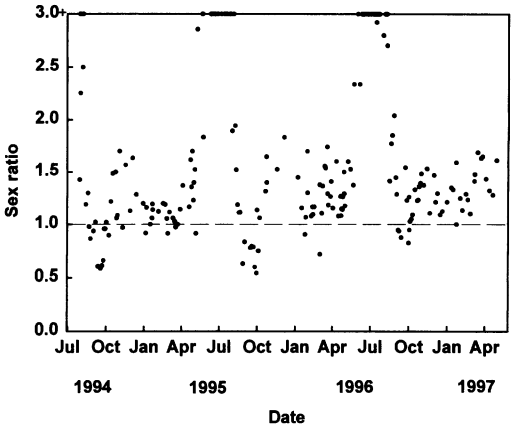

FIG. 2. Sex ratio (males per female) of Harlequin Ducks at White Rock, British Columbia. Values larger than 3.1 are presented as 3.0+ at the top of the figure.

ed. At this time, the sex ratio was female biased (Fig. 2). Large numbers of mostly unpaired males were observed sporadically in April; these birds did not molt at the study area. Pairs departed for the breeding grounds starting in April, and by mid-May most birds were gone. The sex ratio usually was male biased in late fall and winter, ranging up to two males per female (Fig. 2).

Within-season movements.—Before pair bonds formed, males ranged over a larger area than did females (Table 1). Likewise, males that were later successful in obtaining a mate were seen over a larger area than males that did not find a mate, although only the 1995 comparison was significant (Table 2). After pair bonds formed, males that were unsuccessful in obtaining a mate were seen over a larger area than paired males in two of three years (Table 2). Males known to be paired in one year and unpaired the next were used to test whether the differ-

TABLE 1. Mean variance (90% CI in parentheses) in the distances over which individually marked male and female Harlequin Ducks were seen within the study area before the onset of pair formation in the beginning of October.

Year	Males			Females				
	n		Variance (km²)	n		Variance (km²)	t	P
1994	39		5.2(0.0 to 17.2)	15		0.8(0.0 to 3.6)	3.68[a]	0.0006[b]
1995	35		5.2(0.0 to 13.1)	35		0.9(0.0 to 7.1)	3.27	0.0017[b]
1996	38		4.5(0.0 to 10.4)	22		1.2(0.0 to 3.5)	5.26[a]	0.0001[b]

[a] Value adjusted for unequal variances between groups ($P < 0.0001$).
[b] Significant after sequential Bonferroni adjustment at $\alpha = 0.05$ (Rice 1989).

TABLE 2. Mean variance (90% CI in parentheses) in the distances over which individually marked male Harlequin Ducks were seen within the study area. Data are divided into males that subsequently were paired vs. unpaired. Harlequin Ducks begin pair formation in the beginning of October.

Year	Subsequently paired		Unpaired		t	P
	n	Variance (km²)	n	Variance (km²)		
		1 June to 1 October				
1994	18	6.5 (0.0 to 23.6)	7	3.5 (0.0 to 10.1)	1.18[a]	0.248
1995	19	6.4 (0.0 to 16.7)	7	2.4 (0.9 to 3.9)	3.10[a]	0.006[b]
1996	13	5.1 (0.0 to 13.9)	8	3.4 (0.0 to 9.9)	0.87	0.395
		1 October to 31 May				
1994	21	2.2 (0.0 to 7.2)	7	6.2 (0.0 to 12.8)	3.23	0.003[b]
1995	22	3.8 (0.0 to 12.7)	5	7.4 (0.0 to 12.8)	1.75	0.091
1996	16	3.1 (0.0 to 10.9)	9	9.5 (0.0 to 19.9)	3.20	0.004[b]

[a] Value adjusted for significantly unequal variances between groups ($P < 0.026$).
[b] Significant after sequential Bonferroni adjustment at $\alpha = 0.05$ (Rice 1989).

ence in movement patterns of males resulted from a difference between males in these two groups, or whether a male's success in finding a mate eventually influenced his movement patterns. Five males that were paired in one year and not paired the next year were seen over a larger area when they were unpaired (mean variance = 9.2 km², 90% CI = 0.1 to 18.3 km²) than when they were paired (mean variance = 2.6 km², 90% CI = 0 to 11.9 km²; paired $t = 2.43$, $P = 0.04$).

Are males territorial?—If individual males were defending territories, they should have distributed themselves across the available habitat with little or no overlap in spatial use among adjacent birds. Although males were spread out across the habitat, oftentimes several males were present simultaneously along a given section of shoreline (Fig. 3), which indicated that males were not territorial.

Winter philopatry.—We detected no annual differences in return rates for either sex (Fisher's exact test, $P > 0.10$), so data were pooled across years. We found no difference in the propensity for different age classes to return from one year to the next for males (2 of 4 young birds vs. 61 of 78 older birds; Fisher's exact test, $P = 0.23$) or females (10 of 16 young birds vs. 31 of 50 older birds; $P = 1.00$). Although the return rate of males (76.8%, $n = 82$) was higher than that of females (62.1%, $n = 66$), the difference was not quite significant (Fisher's exact test, $P = 0.07$).

We found no difference in the proportion of paired males (86.1%, $n = 43$) and unpaired males (66.7%, $n = 15$) that returned to the study area in the next year (Fisher's exact test, $P =$ 0.13). However, males that obtained mates had a higher tendency to remain in the study area until spring (97.3%, $n = 37$) than did males that did not obtain a mate the previous year (30%, $n = 10$; Fisher's exact test, $P = 0.0001$).

Individuals were philopatric not only to the general study area, they also tended to use the same section of shoreline within the study area. Repeatability for the annual mean location of each bird was high, ranging from 0.74 to 0.98 ($P < 0.0001$ in all cases) for the two sexes before and after the formation of pair bonds.

DISCUSSION

Resource defense or mate defense?—The number of males observed at the study area was more variable than the number of females, and males that were unsuccessful in obtaining mates were seen across larger areas. These observations are consistent with both a resource-defense and a mate-defense mating system. If the mating system is resource defense, unsuccessful males could be floaters, and if the mating system is mate defense, they could be scrambling for mates. The observation that a number of paired males used the same sections of habitat is compelling evidence that males are not territorial. Thus, a basic condition for territoriality was not met, insofar as males did not exclude other males from a specific area (Brown 1964). Although males may avoid each other on a temporal scale, this behavior is not strict territoriality. Furthermore, behavioral observations revealed that paired males were aggressive toward other males only when unpaired males approached to court their mates (Gowans et al.
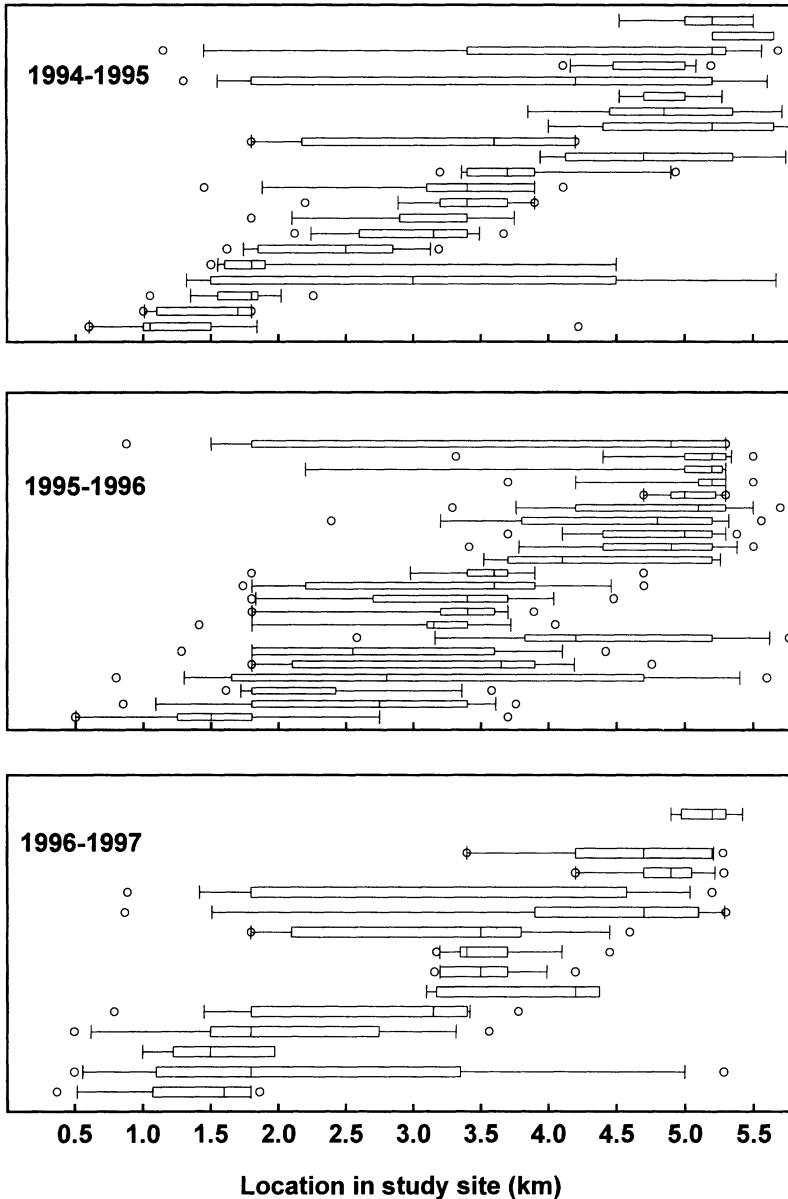
FIG. 3.   Sighting locations of male Harlequin Ducks along a 5.5-km stretch of shoreline for all paired males from 1 October to 1 June. Each row represents a marked individual. Circles denote the 5th and 95th percentiles, whiskers denote the 10th and 90th percentiles, box edges denote the 25th and 75th percentiles, and lines within boxes denote medians.

1997). This behavior is more consistent with mate guarding than with territoriality. Males tended to be clumped during the period before pair formation (Cooke et al. 1997), and we observed very little agonistic behavior at this time. Our observations of wintering Harlequin Ducks suggest that they have a mate-defense mating system, which is the same pattern they show on the breeding grounds (Inglis et al. 1989).

Site fidelity and annual patterns of return.— Within years, both sexes tended to remain faithful to specific stretches of shoreline. The reason that males and females exhibited equally high levels of site fidelity probably was related to the timing of pair formation and the

fact that pairs reunited each year (Gowans et al. 1997). Pair bonds between reuniting birds formed in early fall, generally in October (Robertson et al. 1998). Once the pair bond was re-established, movements of the male and female coincided. Assuming that a male's only concern was maintaining the pair bond, then the high within-season site fidelity shown by Harlequin Ducks likely was due to the advantages of site fidelity for the female. Male Harlequin Ducks that were unsuccessful in obtaining mates, or that lost their mates, roamed about the study area and joined parties of courting bachelor males (Gowans et al. 1997).

Both male and female Harlequin Ducks exhibited high levels of philopatry to their non-breeding grounds. For a long-lived species such as Harlequin Ducks (Goudie et al. 1994), knowledge gained at a wintering site in one year could be used in subsequent years. The little information that is available from other species of sea ducks shows that both sexes exhibit high levels of winter philopatry (Limpert 1980). The difference between return rates of males (77%) and females (62%) in our study may be a function of survival differences rather than levels of philopatry. Female ducks generally suffer higher mortality than males during the period that they are incubating their clutches (Sargeant and Raveling 1992), and female Harlequin Ducks occasionally are killed on the nest (Bruner 1997). Bruner (1997) estimated that survival of adult females during summer was 82% in Oregon, and D. Esler (pers. comm.) estimated that overwinter survival of females was 87% in Alaska; these estimates combine for an annual survival rate of 71%. Unfortunately, there are no estimates for survival of adult males.

Harlequin Ducks probably enjoy advantages from site familiarity such as knowledge of food resources and predators. In addition, because pairs of Harlequin Ducks reunite each fall (Gowans et al. 1997, Robertson et al. 1998), males may return to the same nonbreeding area year after year. For ducks in which the female alone incubates the clutch and raises the brood, males and females must be philopatric to molting, wintering, or breeding sites to be able to reunite (Savard 1985, Gauthier 1987, Williams and McKinney 1996). It is not known whether winter philopatry has evolved directly as a mechanism to allow pairs to reunite, or

whether pair reunion evolved after winter philopatry. However, evidence suggests that waterfowl that engage in long-term pair bonds (even after accounting for age) accrue reproductive advantages relative to newly paired individuals (Black et al. 1996, Rees et al. 1996). Male Harlequin Ducks whose mates did not return in the fall and who were unable to find a new mate in the following spring still returned to molt at the same nonbreeding site in the next year. Most females had not yet arrived on the nonbreeding grounds when males began molting (Robertson et al. 1997). Hence, males are probably philopatric to molting grounds for strictly ecological reasons. However, if males form dominance hierarchies among themselves during molt, as we have suggested elsewhere (Cooke et al. 1997), then philopatry to the molting grounds may be sexually selected as well. Most of these unpaired males departed after they molted, presumably to search out a new mate. Failing to find a mate in one year may be a cue for males to move and attempt to find a mate at another site. Many of the males and females (more than 50% in 1994) molted at the study site and then departed for unknown wintering sites (Robertson et al. 1999). Therefore, philopatry to molting sites in male Harlequin Ducks probably has an ecological basis, whereas philopatry to wintering sites may have a further role in finding and retaining a mate.

Harlequin Ducks exhibit a mating system based on mate defense during the time of pair formation, yet adult males do not disperse each year. Reynolds and Cooke (1988) found that male and female Red-necked Phalaropes (*Phalaropus lobatus*), a polyandrous species, were equally likely to return to the breeding grounds. Females are not territorial in this species, but they compete for mates; only males incubate and care for broods. Benefits for females of returning to the breeding grounds, such as experience with local home ranges to aid in competition for mates, are likely to exist (Reynolds and Cooke 1988). As Greenwood (1980) expected, further refinement in the description of the mating system can lead to a better understanding of the philopatric behavior of a species (Waser and Jones 1983, Johnson and Gaines 1990).

In addition to the ecological advantages that long-lived individuals gain from site familiarity, we suggest that Harlequin Ducks are phil-

opatric so they can reunite with their mates. Common Eiders (*Somateria mollissima*) in pair bonds fed more and spent less time in agonistic encounters than did unpaired birds, which allowed females to accumulate more nutrients for breeding (Ashcroft 1976). In addition, females that reunited with previous partners laid earlier than females that formed new pair bonds (Spurr and Milne 1976). Harlequin Ducks that pair early with a known mate may accrue similar benefits.

Geese and swans are also philopatric to their wintering grounds (Raveling 1979, Reed et al. 1998). Because geese and swans remain paired for the entire year, they do not need to reunite, so philopatry to the wintering grounds must have some ecological advantage (e.g. familiarity with good foraging areas or safe roosting sites; Raveling 1979). Philopatry to wintering sites and migration stopovers also has been documented in other species (e.g. McNeil 1982, Faaborg and Arendt 1984, Cantos and Tellería, 1994). The winter period is probably stressful for most bird species because days are short, food is sparse, and weather generally is unfavorable. For species that pair in winter, survival and pair-bond establishment will influence their life-history strategies at that time of year. Therefore, pressures from both sexual and natural selection may account for the observed patterns of philopatry in these species (Robertson and Cooke 1999).

LITERATURE CITED

ANDERSON, M. G., J. M. RHYMER, AND F. C. ROHWER. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. Pages 365–395 *in* Ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

ANDERSON, M. G., AND R. D. TITMAN. 1992. Spacing patterns. Pages 251–289 *in* Ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

ASHCROFT, R. E. 1976. A function of the pair bond in the Common Eider. Wildlfowl 27:101–105.

BLACK, J. M., S. CHOUDBURY, AND M. OWEN. 1996. Do barnacle geese benefit from lifelong monogamy? Pages 91–117 *in* Partnerships in birds: The study of monogamy (J. M. Black, Ed.). Oxford University Press, Oxford.

BREAULT, A. M, AND J.-P. L. SAVARD. 1999. Philopatry of Harlequin Ducks moulting in southern British Columbia. Pages 41–44 *in* Behaviour and ecology of sea ducks (R. I. Goudie, M. R. Petersen, and G. J. Robertson, Eds.). Canadian Wildlife Service Occasional Papers No. 100.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bulletin 76:160–169.

BRUNER, H. 1997. Habitat use and productivity of Harlequin Ducks in the central Cascade Range of Oregon. M.S. thesis, Oregon State University, Corvallis.

CANTOS, F. J., AND J. L. TELLERÍA. 1994. Stopover site fidelity of four migrant warblers in the Iberian Peninsula. Journal of Avian Biology 25:131–134.

CLARKE, A. L., B.-E. SÆTHER, AND E. RØSKAFT. 1997. Sex biases in avian dispersal: A reappraisal. Oikos 79:429–438.

COOKE, F., G. J. ROBERTSON, R. I. GOUDIE, AND W. S. BOYD. 1997. Molt and the basic plumage of male Harlequin Ducks. Condor 99:83–90.

EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

FAABORG, J., AND W. J. ARENDT. 1984. Population size and philopatry of winter resident warblers in Puerto Rico. Journal of Field Ornithology 55:376–378.

GAUTHIER, G. 1987. Further evidence of long-term pair bonds in the ducks of the genus *Bucephala*. Auk 104:521–522.

GOUDIE, R. I., AND C. D. ANKNEY. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67:1475–1482.

GOUDIE, R. I., S. BRAULT, B. CONANT, A. V. KONDRATYEV, M. R. PETERSEN, AND K. VERMEER. 1994.

The status of sea ducks in the north Pacific Rim: Towards their conservation and management. Transactions of the North American Wildlife and Natural Resource Conference 59:27–49.

GOWANS, B., G. J. ROBERTSON, AND F. COOKE. 1997. Behaviour and chronology of pair formation by Harlequin Ducks Histrionicus histrionicus. Wildfowl 48:135–146.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1–21.

INGLIS, I. R., J. LAZARUS, AND R. TORRANCE. 1989. The pre-nesting behaviour and time budget of the Harlequin Duck Histrionicus histrionicus. Wildfowl 40:55–73.

JOHNSON, M. L., AND M. S. GAINES. 1990. Evolution of dispersal: Theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics 21:449–480.

LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs 62:67–118.

LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. Auk 104: 116–121.

LIMPERT, R. J. 1980. Homing success of adult Buffleheads to a Maryland wintering site. Journal of Wildlife Management 44:905–908.

MCKINNEY, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks. Pages 153–171 in Ecological aspects of social evolution (D. I. Rubenstein and R. W. Wrangham, Eds.). Princeton University Press, Princeton, New Jersey.

MCNEIL, R. 1982. Winter resident repeats and returns of austral and boreal migrant birds banded in Venezuela. Journal of Field Ornithology 53: 125–132.

MYERS, J. P., P. G. CONNORS, AND F. A. PITELKA. 1979. Territoriality in non-breeding shorebirds. Pages 231–246 in Shorebirds in marine environments (F. A. Pitelka, Ed.). Studies in Avian Biology No. 2.

ORING, L. W., AND R. D. SAYLER. 1992. The mating systems of waterfowl. Pages 190–213 in Ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

PETERSON, S. R., AND R. S. ELLARSON. 1978. Bursae, reproductive structures, and scapular color in wintering female Oldsquaws. Auk 95:115–121.

POLLOCK, K. H., J. D. NICHOLS, J. E. HINES, AND C. D. BROWNIE. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs No. 107.

RAPPOLE, J. H., AND D. W. WARNER. 1980. Ecological aspects of migrant behavior in Veracruz, Mexico. Pages 353–392 in Migrant birds in the Neotropics: Ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington D.C.

RAVELING, D. G. 1979. Traditional use of migration and winter roost sites by Canada Geese. Journal of Wildlife Management 43:229–238.

REED, E. T., E. G. COOCH, R. I. GOUDIE, AND F. COOKE. 1998. Site fidelity of Black Brant staging in the Strait of Georgia, British Columbia. Condor 100: 426–437.

REES, E. C., P. LIEVESLEY, R. A. PETTIFOR, AND C. M. PERRINS. 1996. Mate fidelity in swans: An interspecific comparison. Pages 118–137 in Partnerships in birds: The study of monogamy (J. M. Black, Ed.). Oxford University Press, Oxford.

REYNOLDS J. D., AND F. COOKE. 1988. The influence of mating systems on philopatry: A test with polyandrous Red-necked Phalaropes. Animal Behaviour 36:1788–1795.

RICE W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

ROBERTSON, G. J., AND F. COOKE. 1999. Winter philopatry in migratory waterfowl. Auk 116:20–34.

ROBERTSON, G. J., F. COOKE, R. I. GOUDIE, AND W. S. BOYD. 1997. The timing of arrival and moult chronology of Harlequin Ducks Histrionicus histrionicus. Wildfowl 48:148–155.

ROBERTSON, G. J., F. COOKE, R. I. GOUDIE, AND W. S. BOYD. 1998. The timing of pair formation in Harlequin Ducks. Condor 100:551–555.

ROBERTSON, G. J., F. COOKE, R. I. GOUDIE, AND W. S. BOYD. 1999. Within-year fidelity of Harlequin Ducks to a moulting and wintering area. Pages 45–51 in Behaviour and ecology of the sea ducks (R. I. Goudie, M. R. Petersen, and G. J. Robertson, Eds.). Canadian Wildlife Service Occasional Paper No. 100.

ROHWER, F. C., AND M. G. ANDERSON. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. Current Ornithology 5:187–221.

SARGEANT, A. B., AND D. G. RAVELING. 1992. Mortality during the breeding season. Pages 396–422 in Ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

SAVARD, J.-P. L. 1985. Evidence of long-term pair bonds in Barrow's Goldeneye (Bucephala clangula). Auk 102:389–391.

SAVARD, J.-P. L. 1988. Winter, spring and summer territoriality in Barrow's Goldeneye: Character-

istics and benefits. Ornis Scandinavica 19:119–128.

SPURR, E. B., AND H. MILNE. 1976. Adaptive significance of autumn pair formation in the Common Eider *Somateria mollissima* (L.). Ornis Scandinavica 7:85–89.

STEWART-OATEN, A. 1995. Rules and judgments in statistics: Three examples. Ecology 76:2001–2009.

TURPIE, J. K. 1995. Non-breeding territoriality: Causes and consequences of seasonal and individual variation in Grey Plover *Pluvialis squatarola* behaviour. Journal of Animal Ecology 64:429–438.

WASER, P. M., AND W. T. JONES. 1983. Natal philopatry among solitary mammals. Quarterly Review of Biology 58:355–390.

WILLIAMS, M., AND F. MCKINNEY. 1996. Long-term monogamy in a river specialist: The Blue Duck. Pages 73–90 *in* Partnerships in birds: The study of monogamy (J. M. Black, Ed.). Oxford University Press, Oxford.

Associate Editor: T. W. Arnold