HOME RANGES OF SYMPATRIC BLACK AND TURKEY VULTURES IN SOUTH CAROLINA

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Abstract.   We examined home-range characteristics of seven Black Vultures (*Coragyps atratus*) and four Turkey Vultures (*Cathartes aura*) at the Savannah River Site, South Carolina. Birds were captured at their primary roost and tracked via aerial telemetry from 11 February 2002 through 29 January 2003. Mean annual home-range sizes (95% fixed kernel) for Black and Turkey Vultures were 12 399 ± 5199 ha [SE] and 34 053 ± 8567 ha, respectively. Black Vultures concentrated their movements around the primary roost, whereas Turkey Vultures demonstrated less site fidelity. Home-range sizes and time spent soaring for both species were much greater than reported for vultures residing in an agricultural landscape. We suggest that food resources at the heavily forested Savannah River Site were fewer and less predictable than in agricultural landscapes, requiring larger home ranges and increased time spent foraging.

Key words: aerial telemetry, Black Vulture, Cathartes aura*,* Coragyps atratus*, home range, movement patterns, Turkey Vulture.*

Rangos de Hogar de los Buitres Simpátricos *Coragyps atratus* y *Cathartes aura* en Carolina del Sur

Resumen.   Examinamos las características de los rangos de hogar de siete *Coragyps atratus* y cuatro *Cathartes aura* en Savannah River, Carolina del Sur. Las aves fueron capturadas en sus sitios de descanso principales y fueron rastreadas mediante telemetría aérea desde el 11 de febrero de 2002 hasta el 29 de enero de 2003. Los tamaños medios de rango de hogar (kernel fijo del 95%) fueron de 12 399 ± 5199 ha [EE] para *C. atratus* y de 34 053 ± 8567 ha para *C. aura*. *Cathartes atratus* concentró sus movimientos alrededor de sus sitios de descanso principales, mientras que *C. aura* demostró menor fidelidad al sitio. Para las dos especies, los tamaños del rango de hogar y el tiempo que permanecieron planeando fueron mucho mayores que los reportados para buitres que habitan paisajes agrícolas. Sugerimos que en Savannah River, un sitio con alta cobertura forestal, los recursos alimenticios eran más escasos y menos predecibles que en paisajes agrícolas, requiriendo rangos de hogar mayores y un incremento en el tiempo de forrajeo.

Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) are scavengers found commonly throughout much of the temperate and tropical Americas. Both species preferentially use a mosaic of habitat types: roosts and nests often are located in dense, undisturbed forests, whereas pastures, fields, and other open areas are preferred for foraging (Coleman and Fraser 1989, Kirk and Mossman 1998, Buckley 1999). As is evident from the wide distribution and abundance of Black and Turkey Vultures throughout the New World (Kirk and Mossman 1998, Buckley 1999), both species have adapted well to landscapes fragmented by human activities. However, little information is available concerning the spatial ecology of Black or Turkey Vultures across ecosystem types and locations. In particular, virtually nothing is known about home-range characteristics of either species, apart from one study in an agricultural landscape in southern Pennsylvania and northern Maryland (Coleman and Fraser 1989). New information on home ranges and movement patterns of Black and Turkey Vultures would help provide a more complete account of the natural history of these species.

A deeper understanding of the spatial ecology of Black and Turkey Vultures also might aid in reducing bird-aircraft collisions, which cost $400 million annually in aircraft repairs and have been responsible for over 350 human mortalities worldwide (Sodhi 2002). Black and Turkey Vultures together were ranked as the top threat to civil and military aviation with regard to bird–aircraft collisions in the United States (Dolbeer et al. 2000). Accurate information regarding movement patterns of vultures relative to areas of high density and activity (i.e., roosts) might be used to fine-tune spatial models designed to prevent bird–aircraft collisions.

The purpose of this study was to quantify home-range characteristics of Black and Turkey Vultures at a heavily forested site in South Carolina where both species are common. We used radio-telemetry from fixed-wing aircraft to observe individuals of both species over a year. A primary objective was to compare our results to those of Coleman and Fraser (1989), allowing a comparison of home-range ecology in two

very different landscapes. Secondarily, we examined the time spent soaring as opposed to other activities, flight altitudes, and the nature of vulture movements with regard to the major communal roost.

METHODS

STUDY AREA

The 78 000 ha Savannah River Site is a limited-access nuclear production and research facility near Aiken, South Carolina. The Savannah River Site is owned and operated by the United States Department of Energy. Approximately 64% of the site has been planted in loblolly pine (*Pinus taeda*), longleaf pine (*P. palustris*), and slash pine (*P. elliottii*; Workman and McLeod 1990), which are managed for timber by the United States Forest Service. An additional 15% of the land cover is classified as bottomland hardwood (Workman and McLeod 1990). Although most of the Savannah River Site is forested, several industrial areas are located throughout the site. Elevation ranges from <30 m above sea level on the southwestern portion of the site to 115 m on the northern portion of the site (White and Gaines 2000).

FIELD METHODS

In 2000 and 2001 we captured 22 Black Vultures and 12 Turkey Vultures, primarily by rocket net. All individuals were captured near R-Reactor, an abandoned nuclear reactor located approximately 5 km east of the center of the Savannah River Site. R-Reactor has served as a major communal vulture roost for many years (ILB, pers. obs.).

Captured birds were weighed and aged (adult or juvenile) based on the color and degree of wrinkling of the head (Kirk and Mossman 1998, Buckley 1999). Backpack-style radio-transmitters weighing ~30 g (Holohil Systems Ltd., Carp, Ontario, Canada; model AI-2B; 164–166 MHz) were attached to all birds. The transmitters were equipped with position sensors that enabled us to determine remotely whether radio-tagged birds were oriented horizontally or vertically. Transmitters always emitted the horizontal signal when radio-tagged birds were in flight. Transmitters on perched birds usually emitted the vertical signal; however, occasionally the horizontal signal was emitted during feeding or loafing.

A preliminary examination of telemetry error at the Savannah River Site indicated that radio-tracking from ground level was not feasible for such wide-ranging birds due to extensive forest cover and the lack of an extensive road network in some areas (White and Gaines 2000). Thus, we conducted a detailed study to evaluate the feasibility of aerial telemetry and to assess patterns of error (DeVault et al. 2003). We used a fixed-wing aircraft (Cessna 172) equipped with a two-element Yagi antenna on each wing strut to locate 24 beacons (vulture transmitters) placed throughout the Savannah River Site and to mark their locations with a handheld GPS receiver. We found that the mean linear distance error (from actual beacon locations to locations estimated via aerial telemetry) was 191 ± 197 m (SD; range 22–1011 m), and that 95% confidence circles were 47 ha in size. Twenty-two of 24 (92%) of the actual beacon locations fell within the confidence

circles. These error estimates fell within the normal bounds for aerial telemetry (Samuel and Fuller 1996) and provided a reasonable degree of accuracy for our objectives (DeVault et al. 2003). However, the error estimates applied only to location estimates of unseen, perched birds. Although we could not quantify the linear error associated with location estimates of visible perched or soaring birds (see below), such location estimates were almost certainly more accurate than those of unseen, perched birds.

We conducted 84 telemetry flights, totaling 175 hr, from 11 February 2002 through 29 January 2003. One radio-tracker accompanied the pilot on all flights. We distributed flight times evenly over all daylight hours. Occasionally, flights were postponed due to rainfall or heavy winds; however, vultures were generally perched and inactive during such times.

During each flight, we systematically searched the Savannah River Site and the surrounding 15 km to locate as many birds as possible during the prearranged flight time (generally 2 hr). Upon detecting a radio signal, the radio-tracker indicated the general direction of that signal to the pilot. If the transmitter emitted a vertical signal (perched bird), we followed steps outlined in Samuel and Fuller (1996) and DeVault et al. (2003) to mark the estimated location with a Garmin 12 CX handheld GPS unit (10–30 m accuracy). Generally, this process entailed (1) circling the signal source, (2) visually estimating the bird's location after circling the signal source several times and monitoring signal strength, and (3) flying directly over the estimated location and recording the coordinates with the GPS unit. If the transmitter emitted a horizontal signal (flying bird), we circled the signal source widely until we visually located the bird, beginning at approximately 1000 m above ground level and descending slowly. When we located the bird visually, we flew at the same altitude as the bird and recorded its altitude using the GPS unit. We verified all altitude estimates generated by the GPS unit with the aircraft's onboard altimeter and found that the estimates were always within 10 m. After we recorded altitude, we flew directly over the marked bird and recorded its location with the GPS. If we could not see a target bird emitting a horizontal signal after ~5 min of searching, we first confirmed that the bird was not above the airplane by tilting the wing tips and monitoring signal strength, and then proceeded to locate the bird under the assumption that it was perched. Individual birds were not located more than once per telemetry flight.

STATISTICAL ANALYSES

Eleven Black Vultures and six Turkey Vultures apparently left the vicinity of the Savannah River Site shortly after trapping. Some birds captured during the winter were likely migrant birds that returned to more northern locations in the spring. Other birds may have used the R-Reactor only as a secondary roost. Additionally, two radio-tagged Black Vultures and one radio-tagged Turkey Vulture died from unknown causes during the study period. Thus, we restricted our analyses to seven Black Vultures and four Turkey Vultures that were located >30 times throughout the tracking period. Restricting our analyses to these birds helped assure that we only considered birds whose home rang-

TABLE 1.   Home-range characteristics of Black Vultures and Turkey Vultures at the Savannah River Site, South Carolina. Home-range sizes (ha) were calculated by 50% fixed kernel, 95% fixed kernel, and 95% Jennrich-Turner (JT) methods. Interspecific comparisons of home-range sizes were conducted using Mann-Whitney U-tests. Data were gathered via aerial telemetry from 11 February 2002 through 29 January 2003.

| | | Mass | | | Home-range size | |
Individual	Age[a]	(kg)	n[b]	50% kernel	95% kernel	95% JT
Black Vulture						
A	Adult	2.4	50	1509	4579	6067
B	Adult	2.3	42	1516	5365	42 071
C	Adult	2.4	47	1557	6308	43 828
D	Adult	2.4	35	1470	4209	1004
E	Adult	1.8	40	1674	7788	9266
F	Adult	2.4	47	3722	41 418	81 688
G	Adult	2.2	45	2749	17 128	45 337
Mean ± SE		2.3		2028 ± 330+	12 399 ± 5119+	32 751 ± 10 948*
Turkey Vulture						
H	Adult	2.1	47	1811	9117	88 804
I	Juvenile	2.0	51	2424	38 699	62 690
J	Adult	1.7	36	4918	40 236	54 505
K	Adult	2.0	50	7485	48 161	80 195
Mean ± SE		2.0		4159 ± 1296+	34 053 ± 8567+	71 549 ± 7861*

[a] Determined based on the color and degree of wrinkling of the head (Kirk and Mossman 1998, Buckley 1999).
[b] Number of telemetry locations.
+ $P < 0.10$; * $P < 0.05$.

es were confined to the tracking area, and that stable home-range estimates were generated (Seaman et al. 1999, Kernohan et al. 2001).

We calculated home-range estimates using the fixed kernel method described by Worton (1989, 1995). We used the least-squares cross-validation procedure to choose the optimal smoothing parameter. Following Churchill et al. (2002), we calculated the smoothing parameters at 50% and 95% utilization distribution levels separately for each bird, and then used the median value of the smoothing parameters from the initial calculations for all subsequent analyses. We also calculated noncircular home ranges using the Jennrich-Turner estimator (Jennrich and Turner 1969) to allow comparison with vulture home-range estimates from Coleman and Fraser (1989).

We used Mann-Whitney U-tests to examine interspecific differences among home-range sizes based on 50% kernel, 95% kernel, and 95% Jennrich-Turner home-range descriptors (Table 1). We used the Animal Movements extension (Hooge and Eichenlaub 1997) in ArcView 3.2 (ESRI 1999) to generate all home-range estimates, and SPSS version 10.0 (SPSS 1999) for statistical analyses.

RESULTS

We obtained 490 location estimates (306 from Black Vultures and 184 from Turkey Vultures) from the 11 birds located >30 times. For Black Vultures, 169 (55%) of the location estimates were of soaring birds. Of the 137 location estimates of perched Black Vultures, 59 (43%) were visually obtained. For Turkey Vultures, 111 of the location estimates (60%) were of

soaring birds. Of the 73 location estimates of perched Turkey Vultures, 23 (32%) were visually obtained. All unseen birds were assumed to be perched. The mean flight altitude (above ground level) for Black Vultures and Turkey Vultures was 166 ± 115 m (SD; $n = 169$) and 165 ± 93 m ($n = 111$), respectively.

The mean home-range size of Turkey Vultures was over twice that of Black Vultures for 50% kernel, 95% kernel, and 95% Jennrich-Turner methods (Table 1). However, only the home-range estimates calculated by the Jennrich-Turner method were significantly different between species at $\alpha = 0.05$ (Table 1).

Despite the large size of the Savannah River Site (78 000 ha), 139 of 306 (45%) location estimates for Black Vultures were within 1 km of the R-Reactor (Fig. 1). The two Black Vultures whose home ranges did not include the R-Reactor (individuals E and G; Fig. 1) also concentrated their movements around a communal roost. Individual E's home range was centered on a 40-m-tall fire tower that traditionally has served as a vulture roost near the town of Jackson, South Carolina. Individual G's home range included several nuclear industrial areas that occasionally served as roosts. In contrast, only 33 of 184 (18%) location estimates of Turkey Vultures were within 1 km of the R-Reactor. Like Black Vultures, all core home ranges of Turkey Vultures included a communal roost.

DISCUSSION

Vultures at the heavily forested Savannah River Site exhibited annual home ranges about twice as large as those reported by Coleman and Fraser (1989) in south-
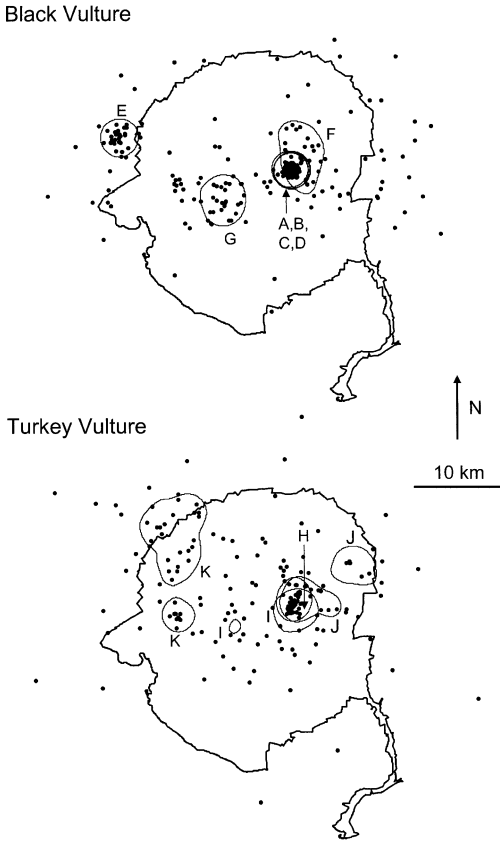
Black Vulture

Turkey Vulture

FIGURE 1.   Location estimates and 1-year core home ranges (50% fixed kernel) of seven Black Vultures (*n* = 306 locations) and four Turkey Vultures (*n* = 184 locations) at the Savannah River Site, South Carolina. Locations were estimated by fixed-wing aerial telemetry from 11 February 2002 through 29 January 2003. Four of the core home ranges for Black Vultures were nearly identical in size and location, reflecting the intense use of the immediate vicinity of the R-Reactor, the main communal roost. Letters correspond to the individuals in Table 1; the heavy black line indicates the boundary of the Savannah River Site.

ern Pennsylvania and northern Maryland. In Coleman and Fraser's (1989) study, Black and Turkey Vultures had annual home ranges (Jennrich-Turner method) of 14 881 ± 3160 ha (SE; *n* = 5) and 37 072 ± 27 625 ha (*n* = 4), respectively, compared to our estimates of 32 751 ± 10 948 (*n* = 7) and 71 549 ± 7861 (*n* = 4) using the same home-range calculation method. Our ability to locate vultures far from the main roost using aircraft might have contributed somewhat to the larger home-range estimates we obtained compared to those reported by Coleman and Fraser (1989), who tracked from a car. Nonetheless, the magnitude of difference in home-range sizes between the two studies strongly suggests that Black and Turkey Vultures have considerably larger home ranges at the Savannah River Site

than in southern Pennsylvania and northern Maryland. To our knowledge, the only other published home-range study of Black or Turkey Vultures was conducted by Santana et al. (1986) in southern Puerto Rico; they reported an 18-month home-range size (minimum polygon method; Mohr 1947) of 45 800 ha for one radio-tagged Turkey Vulture.

In a recent review, Rolando (2002) concluded that food availability is generally the most important determinant of home-range size and shape in birds. Our study appears to support this assertion, as the differences in home-range size between the current study and that by Coleman and Fraser (1989) probably reflect variations in habitat structure, and thus feeding opportunities, between the two sites. Black and Turkey Vultures in Pennsylvania and Maryland primarily used carcasses of domestic animals generated by the numerous cattle, hog, poultry, and dairy farms located throughout the mostly agricultural landscape (Coleman and Fraser 1987). Conversely, feeding opportunities at the Savannah River Site, which is ~80% forested, are almost certainly fewer and less predictable. Our anecdotal observations suggest that Savannah River Site vultures make extensive use of road-killed animals (especially white-tailed deer [*Odocoileus virginianus*]); however, Savannah River Site vultures apparently must range wider than those in agricultural landscapes to forage adequately.

Black and Turkey Vultures at the Savannah River Site also were observed soaring more frequently than their counterparts in Pennsylvania and Maryland. In Coleman and Fraser's (1989) study, Black and Turkey Vultures spent 9–12% and 27–33% of daylight hours in flight, respectively. Conversely, Savannah River Site vultures flew during the majority of daylight hours (55% for Black Vultures and 60% for Turkey Vultures). Greater time spent in flight for Savannah River Site vultures compared to those in Pennsylvania and Maryland lends further support to our assertion that foraging was less predictable and more time-consuming for vultures at the heavily forested Savannah River Site. Coleman and Fraser (1989) did not quantify flight altitudes of their marked vultures; however, other literature suggests that Black Vultures normally fly substantially higher than Turkey Vultures, and that Turkey Vultures usually fly below 150 m except when migrating (Houston 1988, Estrella 1994, Buckley 1996). It appears that vultures at the Savannah River Site, and especially Turkey Vultures, tend to fly higher than vultures in other areas.

Although some aspects of the movements of Black and Turkey Vultures appear to vary depending on habitat structure and foraging opportunities, the use of large communal roosts is prevalent across habitat types (Kirk and Mossman 1998, Buckley 1999). Core home ranges of all radio-tagged Black and Turkey Vultures in this study were centered on a traditional roost, and 8 of 11 included the R-Reactor, the largest communal roost in the Savannah River Site vicinity, where all birds were trapped (Fig. 1). Communal roosts offer advantages to both species, including energy savings through thermoregulation, opportunities for social interactions, and a reduced risk of predation (Buckley 1998, Kirk and Mossman 1998). For Black Vultures,

communal roosts also enhance foraging success by facilitating the formation of foraging groups (Buckley 1996) and by serving as information centers, allowing naïve birds to follow knowledgeable birds to known feeding locations (Rabenold 1987). The use of communal roosts as information centers may be especially advantageous in heavily forested areas like the Savannah River Site where foraging is more difficult (Buckley 1997).

The results of this study and those of Coleman and Fraser (1989) suggest that Black and Turkey Vultures are able to adjust their home ranges, movement patterns, and flight behavior to local conditions, especially those related to habitat structure and foraging opportunities. This plasticity in ranging behavior undoubtedly has contributed to the vast distribution and relative abundance of both species throughout the Americas (Sauer et al. 2003), as well as their recent range expansion into the northeastern United States (Rabenold 1989). Future studies concerning the interplay of ranging behavior, foraging ecology, and flight behavior would identify key elements that control plasticity of vulture movements and provide a more complete assessment of the biology of the two species.

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WINTER PHILOPATRY OF HARLEQUIN DUCKS IN PRINCE WILLIAM SOUND, ALASKA

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Abstract. We used capture-mark-recapture data to assess winter philopatry by Harlequin Ducks (*Histrionicus histrionicus*) in Prince William Sound, Alaska, during winters 1995–1997 and 2000–2001. Philopatry was quantified using homing rates, which were estimated as the proportion of birds recaptured at their original site out of all recaptured birds. Between-year homing rates of 0.95 (95% CI: 0.87–1.00) and 1.00 (0.92–1.00) were estimated for females and males, respectively, at three locations on Montague Island. Similar homing rates were measured in western Prince William Sound, where estimates were 0.92 (0.80–0.98) for females and 0.96 (0.79–1.00) for males, with a scale of detected movements for all recapture birds ranging from 3–52 km. Our results indicate that wintering aggregations may be demographically independent at a much finer spatial scale than genetic data indicate, and that conservation efforts should recognize this degree of demographic separation among population segments.

Key words: demographic independence, Harlequin Duck, Histrionicus histrionicus*, homing rate, seaduck, site fidelity, winter philopatry.*

Filopatría Invernal de *Histrionicus histrionicus* en Prince William Sound, Alaska

Resumen. Utilizamos datos de marcaje y recaptura para determinar la filopatría de *Histrionicus histrionicus* en Prince William Sound, Alaska, durante los inviernos de 1995–1997 y 2000–2001. La filopatría fue cuantificada utilizando la tasa de retorno, estimada a partir de la proporción del total de aves capturadas que se recapturaron en su sitio original. Las tasas de retorno entre años, estimadas en tres localidades en la isla Montague, fueron de 0.95 (95% IC: 0.87–1.00) y 1.00 (0.92–1.00) para hembras y machos, respectivamente. En Prince William Sound se midieron tasas de retorno similares, donde las estimaciones fueron 0.92 (0.80–0.98) para las hembras y 0.96 (0.79–1.00) para los machos, y para todas las aves recapturadas se detectó una escala de movimiento entre 3 y 52 km. Nuestros resultados indican que las agrupaciones de invierno pueden ser demográficamente independientes a una escala espacial mucho más fina de lo que los datos genéticos indican, y que los esfuerzos de conservación deberían reconocer este grado de separación demográfica entre segmentos de poblaciones.

Breeding philopatry among North American waterfowl is typically female biased, and much attention has focused on the social and genetic consequences of this particular sex-biased dispersal pattern (Greenwood 1980, Rockwell and Barrowclough 1987, Rohwer and Anderson 1988). To date, comparatively little attention has been given to the consequences of philopatric behavior during other stages of the annual cycle. However, for most species the winter period encompasses a majority of the annual cycle and can be a considerable source of annual mortality. Furthermore, because most migratory waterfowl form pair bonds on wintering areas, the strength of individual affiliations to specific wintering grounds plays an important role in determining the genetic and demographic structure of populations (Robertson and Cooke 1999).

For example, geese and swans (tribe Anserini) typically exhibit high levels of philopatry to both breeding

and wintering areas. As a result, their populations tend to be among the most genetically and demographically substructured of any migratory bird (Robertson and Cooke 1999), with geographically distinct subpopulations often forming at one or both stages. A classic example is that of the Canada Goose (*Branta canadensis*), for which 12 or more subspecies have been recognized (Van Wagner and Baker 1990, Scribner et al. 2003). In contrast, dabbling duck species (tribe Anatini) exhibit extremely low rates of winter philopatry, particularly among males (Robertson and Cooke 1999). Anatini populations tend to be much more genetically panmictic and demographically interconnected despite high rates of breeding site fidelity (Anderson et al. 1992). The Northern Pintail (*Anas acuta*) offers an extreme example, as they have very low rates of winter philopatry (Fedynich et al. 1989, Hestbeck 1993), with almost no genetic population structuring even at a continental scale (Cronin et al. 1996), and demographic rates that are thought to be correlated across broad geographic regions (Hestbeck 1993).

Seaducks (tribe Mergini) provide an interesting exception to the general pattern of low winter philopatry and male-biased dispersal characteristic of other ducks. Several seaduck species exhibit a high degree of philopatry to nonbreeding areas (Alison 1974, Spurr and Milne 1976, Limpert 1980, Savard 1985, Breault and Savard 1999, Robertson et al. 2000, Flint et al. 2000, Pearce et al. 2004), which makes them a potentially useful group for resolving the ecological mechanisms underlying philopatry, as well as deducing its genetic and demographic consequences. Furthermore, because of conservation concerns brought on by declines in seaduck population numbers (U.S. Fish and Wildlife Service 1993, Goudie et al. 1994), understanding how affinities to specific locations during the annual cycle may act to constrain population growth rates is extremely important.

In this paper we assess philopatry of Harlequin Ducks (*Histrionicus histrionicus*) wintering in Prince William Sound, Alaska (60°N, 148°W). Previous research on the wintering ecology of Harlequin Ducks has indicated that wintering habitats are stable and predictable (Esler, Bowman et al. 2000), and that within-winter site fidelity to specific stretches of coastline is high (Robertson et al. 1999, Cooke et al. 2000). Furthermore, Harlequin Ducks form pairs on wintering areas (Bengston 1972, Gowans et al. 1997, Robertson et al. 1998), re-pairing appears to be common (Smith et al. 2000), and there is evidence that postfledging broods are led to wintering areas by females (Regehr et al. 2001). While much research has been conducted to illuminate these characteristics, formal estimates of winter return rate are few. Winter philopatry has been studied in coastal British Columbia (Robertson et al. 1999, Cooke et al. 2000, Regehr 2003), but no studies have determined whether these patterns are consistent across the species' range. Thus, our objective was to quantify rates of winter philopatry by adult Harlequin Ducks in Prince William Sound, Alaska, and to consider the genetic, demographic, and conservation implications of the observed rates of movement.

METHODS

FIELD METHODS

Harlequin Ducks were captured during wing molt by herding flightless birds into funnel traps using sea kayaks. Unlike most waterfowl, Harlequin Ducks undergo wing molt on the same marine areas where they winter (Robertson and Goudie 1999, although more extensive molt migrations have been documented in the eastern North American population, Brodeur et al. 2002). Therefore, inferences drawn from molting birds are applicable to both molting and wintering stages. Three different trapping locations were used along northwestern Montague Island: (1) Stockdale Harbor, (2) Port Chalmers (3) West Montague (Fig. 1). Distances between sites ranged from 8.4 to 16.1 km. Capture sessions were conducted during five molt seasons: 1995, 1996, 1997, 2000, and 2001. Capture dates ranged from 1 August to 17 September in 1995–1997 and 6 to 12 September in 2000–2001. These capture dates encompassed the periods of peak wing molt by adult females. Adult males typically undergo wing molt before females, and were not targeted during 2000–2001. All captured individuals were marked with U.S. Fish and Wildlife Service aluminum bands. Sex determinations were based on plumage characteristics and cloacal examination. Age class was determined by probing bursal depth (Mather and Esler 1999). Our analyses were restricted to after-hatch-year birds because waterfowl do not undergo a wing molt during their first autumn and, as a result, hatch-year birds were not susceptible to our trapping methodology.

STATISTICAL ANALYSIS

We quantified philopatry by estimating homing rate, which is the probability an individual will return to the study area, given that it is alive. In studies that use multiple capture areas, homing rate can be estimated directly as the ratio of birds recaptured on their original capture site to those recaptured elsewhere (Robertson and Cooke 1999). This ratio considers only individuals alive at both time t and time $t + 1$, thus eliminating survival as a confounding variable. The method assumes that recapture probabilities are similar at all study sites, and will tend to overestimate the true homing rate if recapture effort outside the study area is low. We estimated homing rates and 95% CI for Harlequin Ducks banded and subsequently recaptured at the three capture sites on Montague Island. Contingency tests were used to assess variation in homing rate with respect to sex, trapping location, and year of recapture.

To complement this fine-scale analysis, we used supplementary data from Harlequin Ducks captured in western Prince William Sound, to estimate the number of birds that moved outside the Montague Island study area (a requirement of unbiased homing-rate estimation), and to quantify the range of distances moved. The additional capture sites were located on the Kenai Peninsula (Foul Bay, Main Bay, Crafton Island), Knight Island (Bay of Isles), and Green Island (North Green, West Green, South Green; Fig. 1). All seven of the additional trapping sites were located within the *Exxon Valdez* oil spill zone, and ranged in distance from 8.0–62.4 km from Montague Island. Capture protocols were identical to those described above, and
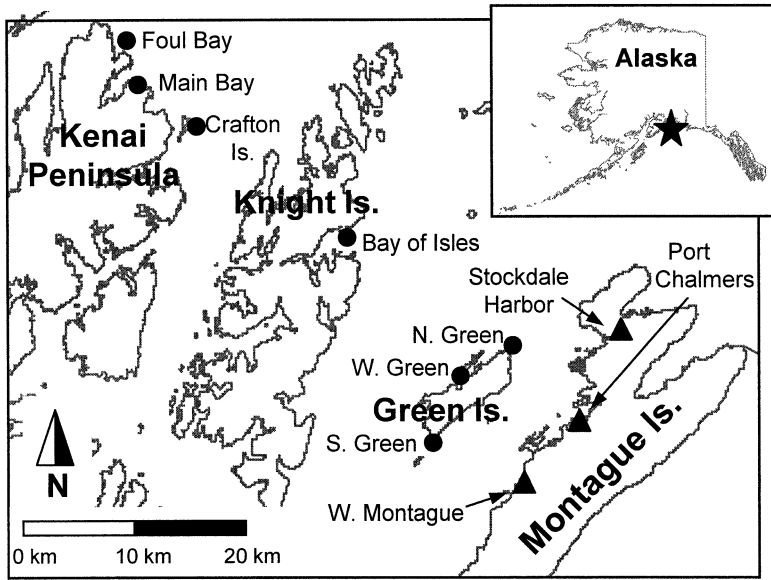
FIGURE 1.   Map of the Harlequin Duck study area in Prince William Sound, Alaska. Triangles denote primary capture locations on Montague Island; circles denote supplementary capture sites on the Kenai Peninsula, Knight Island, and Green Island.

took place over the same date ranges as at Montague Island during 1995, 1996, and 1997.

RESULTS

In total, 799 captures were made during the 5 years of trapping on Montague Island, of which 348 were males and 451 were females. Among these, 102 were recaptures (28 males and 74 females). Homing rates to the three Montague Island capture locations were high, with estimates of 0.95 (95% CI: 0.87–1.00) and 1.00 (0.93–1.00) for recaptured females and males, respectively. Homing rate did not differ according to sex (Ta-

TABLE 1.   Homing rates for adult Harlequin Ducks captured in Prince William Sound, Alaska, during winter. Homing rate was calculated as the number of individuals recaptured at their original banding location divided by the total number recaptured. See Figure 1 for locations of main and supplementary capture sites.

	Number captured	Number recaptured	Homing rate	95% CI
Montague Island capture sites[a]				
Males	348	28	1.00	0.92–1.00
Females	451	74	0.95	0.87–1.00
Supplementary capture sites[b]				
Males	334	24	0.96	0.79–1.00
Females	342	49	0.92	0.80–0.98

[a] Operated 1995–1997 and 2000–2001.
[b] Operated 1995–1997.

ble 1; Fisher exact test, $P = 0.57$), location ($\chi^2_2 = 3.0$, $P = 0.22$), or year ($\chi^2_3 = 3.0$, $P = 0.39$).

An additional 676 after-hatch-year birds, 334 male and 342 female, were captured at the seven trapping locations in western Prince William Sound, including 73 recaptures. Homing rates in western Prince William Sound were estimated at 0.92 ($n = 49$; 95% CI: 0.80–0.98) and 0.96 ($n = 24$; 0.79–1.00), for females and males, respectively. None of the birds originally banded on Montague Island during 1995 or 1996 were recaptured in outlying areas during 1996 or 1997. In the combined datasets, a grand total of 175 after-hatch-year Harlequin Ducks were recaptured, nine of which were at sites other than their original location. The maximum dispersal distance for any bird was 51.9 km, by a female dispersing from Foul Bay on the Kenai Peninsula to the north end of Green Island. The remaining eight recaptures in which movement was detected included one male and seven females, and ranged in distance from 3.1 to 8.9 km.

DISCUSSION

Harlequin Ducks in Prince William Sound, Alaska, exhibited a high degree of philopatry to specific wintering areas. The homing rates calculated in this study were >90% for both sexes, making them among the highest documented of any waterfowl species (Anderson et al. 1992, Robertson and Cooke 1999). The longest recorded dispersal distance was 52 km. Our results corroborate previous work on Harlequin Duck site fidelity and winter philopatry in coastal British Columbia (Robertson and Cooke 1999, Cooke et al. 2000, Robertson et al. 2000, Regehr 2003), and add to the growing body of evidence suggesting that strong affil-

iations to nonbreeding areas are common among seaduck species (Alison 1974, Spurr and Milne 1976, Limpert 1980, Savard 1985, Breault and Savard 1999, Robertson et al. 1999, Flint et al. 2000).

Several ecological mechanisms have been proposed to select for philopatric behavior by wintering waterfowl. Primary among these are knowledge of local food resources, experience with the movements and habits of predators, and advantages conferred when acquiring mates (Robertson and Cooke 1999). Seaducks have high rates of annual survival, relative to other duck species (Livezey 1995), and hence may acquire considerable experience at particular locations. In addition, some seaducks form pairs during fall and early winter, and there is evidence that pairs reunite from one year to the next (Harlequin Ducks: Gowans et al. 1997, Robertson et al. 1998, Smith et al. 2000; Common Eiders [*Somateria mollissima*]: Spurr and Milne 1976, Tiedemann et al. 1999; Barrow's Goldeneye [*Bucephala islandica*]: Savard 1985). High rates of winter philopatry might result from selective pressure to facilitate re-pairing (Robertson et al. 1998). Finally, environmental variability is thought to be linked to philopatry, with philopatry being more likely in birds that use temporally consistent habitats (Flint et al. 2000). The intertidal prey resources Harlequin Ducks rely on are stable and predictable (Esler, Bowman et al. 2000, Esler et al. 2002), and this dependability likely contributes to the fine-scale homing that we observed.

Molecular data have indicated that genetic structure is evident among wintering populations of Harlequin Ducks only on a continental level, with regional populations being effectively panmictic (Lanctot et al. 1999, K. Scribner et al., unpubl. data). However, our results suggest that from a demographic standpoint wintering subpopulations are independent on a much finer scale. We believe it is important to recognize that a lack of genetic differentiation does not necessarily imply demographic panmixia. Population genetic structure reflects a complex interplay between current and historical population size and movements (Avise 2000), and while only a few immigrants per generation can homogenize the genetic variance within a population, similarly low exchange rates would not necessarily link them demographically. Given the homing rates that we estimated and the movements we observed, demographically important levels of isolation may occur within Harlequin Duck populations at a scale of tens to hundreds of kilometers.

The primary implication of philopatry by a migratory species from a conservation standpoint is that habitat perturbations occurring in a location where seasonal affiliations are strong may have long-lasting effects on local populations. From this perspective, actions such as the recent downlisting of the Eastern population of Harlequin Ducks from Endangered to Special Concern status in Canada (Thomas and Robert 2001) appear less well supported. The species was downlisted because new survey data identified a larger, previously unknown wintering population in Greenland. However, the possibility that the populations in eastern North America and Greenland are demographically isolated should be considered. Along the same lines, previous research has shown that recovery of Harlequin Duck populations in areas affected by the 1989 *Exxon Valdez* oil spill was slowed by the high degree of demographic structure among population segments in south-central Alaska (Esler, Schmutz et al. 2000, Esler et al. 2002). In the absence of immigration of adult females from surrounding populations, full recovery of Harlequin Duck populations in oiled areas was likely delayed, even after immediate spill effects had ended (Esler et al. 2002). We conclude that efforts must be made to identify and manage populations primarily according to their degree of demographic separation, basing area-specific management actions on the demographic viability of population segments throughout the annual cycle.

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