



Non-territorial Floaters in Great Horned Owls (*Bubo virginianus*)

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Abstract.—The ecology and behavior of non-territorial owls are basically unknown. I studied the integration of young Great Horned Owls (*Bubo virginianus*) into the territorial breeding population from 1988-1993 in the southwestern Yukon, Canada, during a peak and decline of the population cycle of snowshoe hares (*Lepus americanus*). Fifty-five fledglings were equipped with radio-transmitters that allowed weekly monitoring of individuals for 2-3 years. After a synchronized dispersal phase in each September, 29-45 percent remained within 35 km of their natal territories. Although 15 percent settled in a territory and were capable of reproducing before the end of their first year of life, most of these owls became non-territorial floaters. Several lines of evidence indicated that this behavior was caused by territorial exclusion of breeding pairs. Floaters were secretive and mostly resident within home ranges that were about five times the size of average territories. Movement patterns suggested that floaters were not involved in extra-pair matings, and that floating is not an alternative reproductive strategy. Survival of floaters was very high during peak densities of prey, leading to a proportion of 40-50 percent of non-territorial owls in the population. When numbers of snowshoe hares declined, emigration and mortality rates increased in floaters before territory owners were affected. The results of this study show how a large proportion of secretive floaters can delay the detection of population declines in traditional censuses of territorial birds, and can lead to serious underestimates of the impacts of predation.

Non-territorial 'floaters', which live a secretive life and form a 'shadow population', are well known for some bird species and assumed for many others (Brown 1964, Newton 1992, Smith 1978, Watson and Moss 1970). Sometimes, such 'surplus' birds live in areas separate from breeding territories, and they may become directly observable when they form social groups (Birkhead *et al.* 1986, Charles 1972) or they may be detectable in open habitat (Haller 1996, Hannon and Martin 1996, Jenny 1992, Watson 1985). Most of the knowledge about floaters, however, is indirect and is derived from experimental removals of territory holders (review in Newton 1992). The majority of owl species are territorial, and ecological field studies are usually based on territorial birds.

Very little is known about floaters in territorial owl populations.

The question of why some birds in a population do not establish a territory and do not breed has been approached from several directions. One hypothesis suggests that the social behavior of territory holders prevents them from breeding (review in Newton 1992). Another hypothesis suggests that a non-territorial stage in an individual's life is not the fate of 'doomed surplus' birds, but is an alternative strategy leading to higher fitness than the strategy of breeding early (Smith and Arcese 1989). Two elements could be involved in such a strategy: (i) Life history theory predicts a trade-off between current investment and future survival, and delayed maturation may be particularly successful for long-lived species such as many owls, because they would produce offspring later in life when they are more experienced and have more secure access to resources

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(review in Stearns 1992). (ii) Delayed establishment of a breeding territory is not necessarily an inactive period in reproduction. Male floaters may gain extra-pair copulations without the cost of defending a territory and providing the brood, whereas female non-territorial owls may secretively settle as a secondary mate of a territorial male of high quality (reviews in Birkhead and Møller 1992, Møller 1987, Korpimäki 1988, Korpimäki *et al.* 1996).

How do floaters survive in a territorial owl population? Very little is known about the behavior of non-territorial owls. How vagrant are they? Do they overlap in their space use with territorial owls or are they restricted to undefended habitat? Do they have special behaviors to avoid aggression by territory owners, and how dangerous it is to intrude into defended space? What is the foraging behavior of non-territorial owls, where do they obtain their food, and how do their intake rates compare to territory owners?

Finally, the question of how many floaters live in a territorial owl population arises. Because territorial owls are easier to detect than floaters, most ecological studies on owls are restricted to the territorial fraction of a population. The consequences of varying floater populations are particularly relevant to predation studies, which may underestimate the effects of owls as predators, and to conservation studies, because a pool of non-territorial birds can affect the recovery of populations (Newton 1991) or can mask population declines when census data is based on breeding territories (Franklin 1992, Wilcove and Terborgh 1984).

I studied Great Horned Owls (*Bubo virginianus*) in the boreal forest in the southwest Yukon, Canada. Great Horned Owls are large, long-lived predators feeding mainly on lagomorphs (Donazar *et al.* 1989). They are territorial year-round, and are widely distributed across North and South America (Voous 1988). Occasional irruptions of Great Horned Owls into southern Canada and the northern United States are linked to the decline phase in the 10-year population cycle of snowshoe hares (*Lepus americanus* Erxleben), which is synchronized across boreal Canada and Alaska (Adamcik *et al.* 1978, Houston 1987, Houston and Francis 1995, Keith and Rusch 1989, McInville and Keith 1974, Rusch *et al.* 1972).

The goal of this paper is to present a portrait as comprehensive as possible of floaters in a selected owl species, and to encourage further studies on floaters in territorial owl populations.

METHODS

This study was part of a collaborative project on the dynamics of the boreal forest ecosystem (Krebs *et al.* 1995). We worked at Klwane Lake (60° 57'N, 138° 12'W) in the southwestern Yukon, and our study area comprised 350 km² of the Shakwak Trench, a broad glacial valley bounded by alpine areas to the northwest and southeast. The valley bottom averages about 900 m above sea level and is covered mostly with spruce forest (*Picea glauca* Blake), shrub thickets (*Salix L. spp.*), some aspen forest (*Populus tremuloides L.*), grassy meadows with low shrub (*Betula glandulosa* Raup.), old burns, eskers, marshes, small lakes, and ponds.

The population data of Great Horned Owls span the years 1988-1993, while most other data are from 1989-1992. Great Horned Owls were censused in late winter and early spring on a 100 km² plot within the main study area. Individual pairs were identified when hooting simultaneously with neighbors at dawn and dusk, and obvious disputes between hooting males or pairs were used for the mapping of territorial boundaries. When necessary, playback of calls were used to elicit territorial responses of owners and their neighbors. Most males were individually known, not only because of radio-tagging but also because of their distinctly different hoots. These differences were later verified with sonograms from recordings at the nest (unpubl. data, method as used for *Strix aluco* by Galeotti 1990). Observations of territorial activity were made almost daily from early February until late April (at least 300 hours in each year).

Survival estimates and information on movements were based on individual Great Horned Owls monitored by radio-telemetry. Twenty-one territorial adult owls were captured with mistnets and cage-traps, and 55 owlets were equipped with radio-transmitters before fledging (breakdown of sample sizes in Rohner 1996, 1997). Successful dispersers were later monitored intensively (3 hatched in 1988, 11 in 1989, and 16 in 1990), and 9 remained as non-territorial floaters in the study area. The radios



weighed 50 g including a shoulder harness of teflon ribbon for attachment as a backpack (< 5 percent of body weight, Kenward 1985). Battery life was 2-2.5 years. The radios were equipped with a two-phase activity switch (sensitive to movement and change of angle).

All floaters and territory holders with transmitters were normally monitored once per week (for the presentation of weekly data, locations in addition to the weekly sampling intervals were excluded). Most checks were conducted with hand-held equipment from the Alaska Highway, which follows the valley bottom for the whole length of the study area. In addition, the entire area and its surroundings were searched for radio signals from helicopter or fixed-wing aircraft at least twice per year (in fall after dispersal, and in spring after the onset of breeding).

Telemetry locations were obtained by triangulating owls with hand-held equipment. Topographical maps were used in the field to plot the locations and assess the number of bearings needed for reliable estimates. The triangulations were then analyzed with the program "Locate II" (Nams 1990) for calculating exact locations and distances. Details on median 95 percent-error ellipses (Lenth estimator, Saltz and White 1990) are presented in Rohner (1997). The accuracy of telemetry locations was assessed by triangulating five transmitters that were placed in trees at a height of 4.5-5.5 m. The deviation of these telemetry locations (error area of $0.052 \pm 0.018 \text{ km}^2$) from the site coordinates obtained by GPS (Global Positioning System) was $0.101 \pm 0.027 \text{ km}$.

Home ranges were measured by utilization distributions based on clustering methods, and all calculations were performed using the program "Ranges IV" (Kenward 1990). From a center of closest locations, an increasing percentage of nearest-neighbor locations were added, resulting in a cumulative increase of core area used. Mononuclear clustering was centered around the harmonic mean location only, whereas multinuclear clustering allowed for separate clusters of closest locations. Home range sizes were then derived for different levels of core percentages (Kenward 1987). For the monitoring period in September 1991, three territorial owls were excluded from analysis because of extreme long-distance movements during several days (these extra-territorial movements are described in Rohner 1996).

All arithmetic means are reported with standard errors and all probabilities are two-tailed unless otherwise specified. Correlation coefficients were calculated as Spearman rank correlations. For statistical testing, non-parametric tests were used wherever possible. The testing of bootstrap hypotheses followed the guidelines of Hall and Wilson (1991), and two-sided probabilities were derived from 500 simulations (see also Rohner 1996).

RESULTS

Dispersal of Juveniles and Age at Maturity

Juvenile owls stayed in their natal territories until September, and then rapidly dispersed in the following weeks (table 1). Dispersal dates were delayed when the cyclic population of snowshoe hares started to decline in 1991 ($U = 152, p = 0.01$). By the end of the first week in October 1989 and 1990, only 4 percent (1 of 27) were still in their natal territories. (In 1991, three of seven owls had not left their natal territories by that time but never dispersed and died in the subsequent winter months near where they fledged). Dispersal distances were not significantly different between years (table 1). Of 55 fledglings monitored from 1988-1991, 29-45 percent remained within 35 km of their natal territories. This distance is equivalent to 10-15 territories in diameter.

The long life spans of radio-transmitters allowed us to examine the integration of fledglings into the breeding population. Only 15 percent (3 of 20) settled in territories before the end of their first year of life. None of nine owls that were further monitored to the end of their second year of life settled during that time. Because of the scarcity of such data, some details are given on the three fledglings that became territorial within the study area: In 1988, one female out of three monitored yearlings, settled in late spring 1989, was actively territorial in fall 1989, and bred successfully in 1990 and 1991. In 1990, two female siblings settled immediately in the same fall without any of the extended dispersal movements typical of other radio-tagged juveniles. Both of these siblings fledged young in the following spring.

Hooting Activity

The remaining 85 percent of monitored owls ($n = 20$), which had not settled within 2 years

Table 1.—*Dispersal of juvenile Great Horned Owls (Bubo virginianus) at Kluane Lake, Yukon (Rohner 1996). Data are provided for sample sizes, dispersal dates, median dispersal distances from the nest in early September (2-9 Sept.) and mid-October (14-21 Oct.), and the proportion of juveniles <35 km from their natal territories by the following spring (either becoming territory holders or remaining floaters).*

	1989	1990	1991
Juveniles monitored	11	16	7
Earliest dispersal date	13 Sept	2 Sept	17 Sept
Latest dispersal date	5 Oct	15 Oct	n.a.
Median dispersal date	20 Sept	20 Sept	27 Sept
Dispersal early Sept. (km)	0.6	0.7	0.8
Dispersal mid Oct. (km)	30.6	35+	16.0
Proportion dispersing < 35 km	.45	.37	.29

after dispersal, did not show any sign of hooting or other territorial defense. In order to test whether these non-territorial 'floaters' would normally be included in a census, a number of radio-tagged owls were monitored within hearing range to record their hooting activity from 3 March to 27 April 1990. Hooting activity was measured as the duration of bouts, each of them considered to be finished when more than 5 minutes elapsed between hoots.

Almost all territorial males, and often also females, gave territorial challenges at least for a short time, particularly at dusk and dawn (see also Rohner and Doyle 1992). In 11 territories that were monitored for a total of 32.0 hours between dusk and midnight, all males were recorded giving territorial challenges. Their hooting bouts lasted 26.7 percent of the total time. Of six individual floaters that were monitored for a total of 16.8 hours between dusk and midnight, none of them gave a territorial challenge or any other call.

During the same time period, known territorial and non-territorial owls were tested for their responsiveness to playback. Territorial challenges were broadcast at irregular intervals for a total duration of 20 minutes from a tape-recorder, and each individual was tested in one trial. Seventeen out of 24 territorial males (70.8 percent) responded vocally. Two out of six floaters approached the speaker as concluded from telemetry readings, but none of them responded with a vocal signal that would

have allowed their detection during a standard census (Fisher's Exact Test, $P < 0.01$, $DF = 1$, $n = 30$).

Movements and Residency of Floaters

The movement patterns of territory holders and floaters were substantially different. Territorial owls were extremely restricted in their movements, and distances between weekly locations of > 3 km were exceptional (calculating median weekly movements for each territory owner, the median over these values for 18 birds was 0.95 km). With a median of 2.63 km, the weekly movements of eight floaters were greater than those of 18 territorial owls ($U = 137$, $p < 0.001$, $n = 26$). Non-territorial owls showed a variety of movement patterns involving larger excursions but were overall relatively sedentary (fig. 1). Only about 20 percent of the recorded distances were greater than 10 km from 1 week to another (Rohner 1996), and none of the radio-marked owls became transient floaters that seemed to move continuously through a large region (fig. 2). Typically, a floater would move within an area of about 5-6 times the size of a territory, and then shift to another area over time, sometimes switching between several known areas of similar size (further details on shifts and patchiness in space use in Rohner 1997).

Size of Home Ranges

Based on weekly locations, floaters covered a 90 percent-area of 12.0-48.3 km² in 1990 and

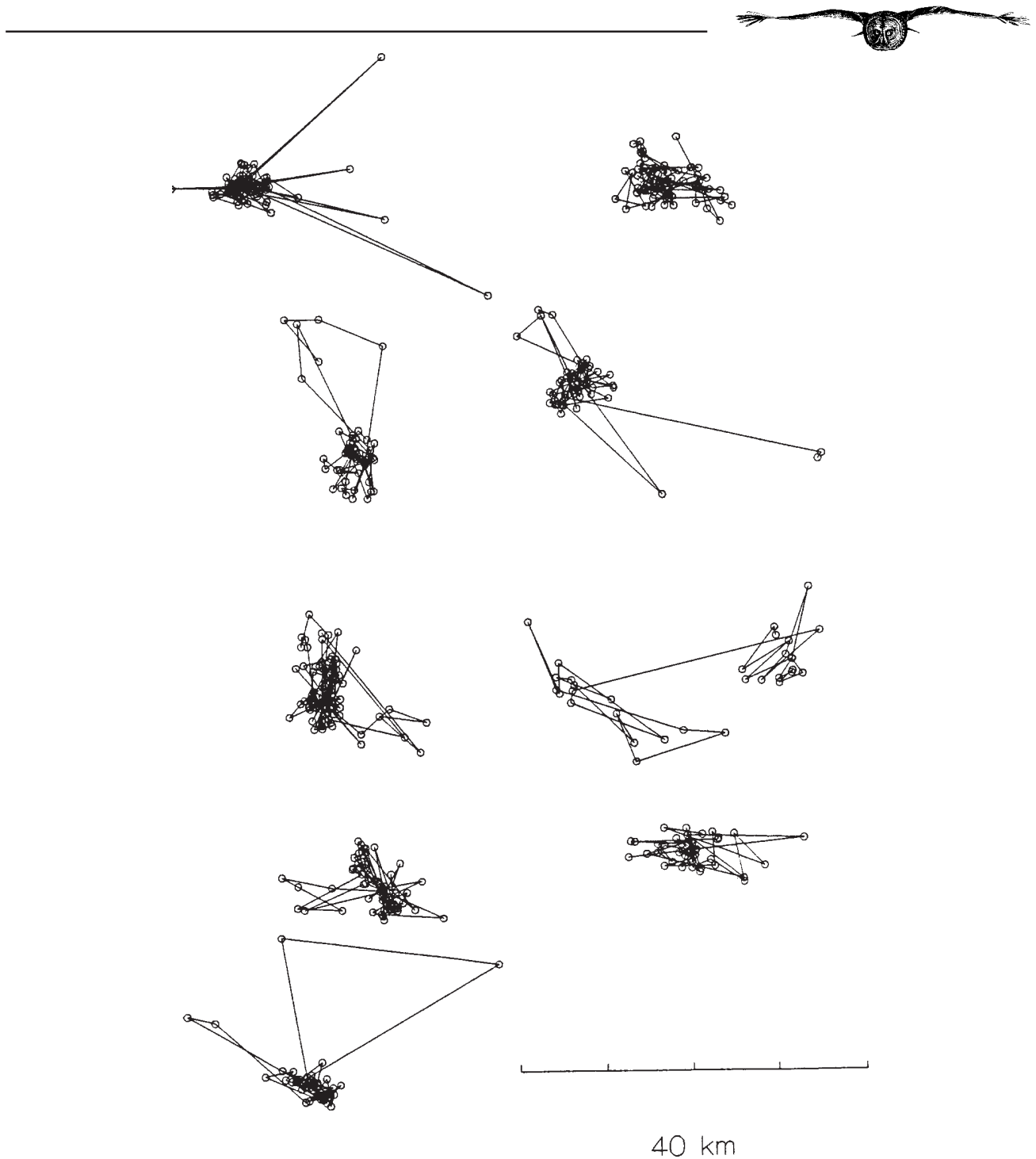


Figure 1.—Weekly locations of nine non-territorial Great Horned Owls (*Bubo virginianus*) during 1990-1992 at Kluane Lake, Yukon (Rohner 1997). The birds are arranged in a panel with the original scale and topographical x-y orientation maintained.

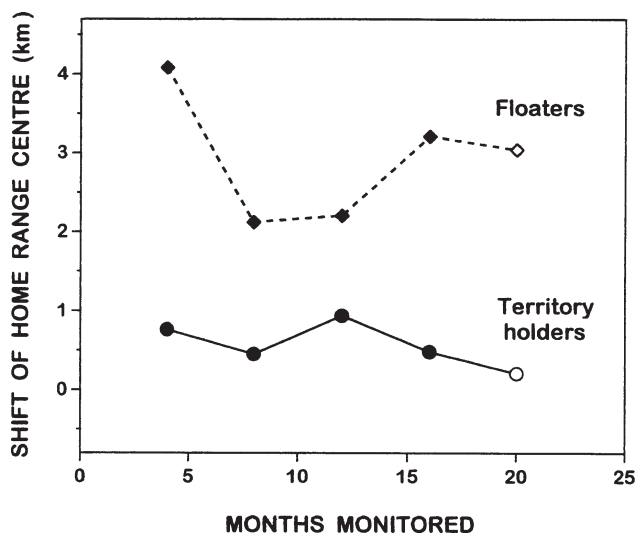


Figure 2.—Median shifts of home range centers, based on all locations, between subsequent 4-month periods of monitoring of floaters and territorial Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon, (Rohner 1997). Filled symbols represent significant differences between the social classes (Mann-Whitney $p < 0.05$). Sample sizes for the time periods were $n_1 = 8, 8, 7, 6, 4$ floaters and $n_2 = 10, 8, 8, 5, 1$ territorial owls.

4.75-69.4 km² in 1991. On average, these values were 26.1 ± 5.7 km² and 24.8 ± 8.1 km². The differences between the 2 years were not significant for 90 percent-area or any other core percentages (Mann-Whitney $U = 24-37$, $p = 0.09-1.00$, $n_1 = 6$, $n_2 = 8$), and the differences were not consistent in any direction for a subsample of individuals that were monitored

through both years (Wilcoxon paired rank-test, $Z = 0.94$, $p = 0.34$, $n = 5$).

Defended territories were much smaller than floater home ranges. In 1990, there were 18-19 territorial pairs per 100 km² (Rohner 1996), i.e., an average territory size of 5.26-5.56 km². In 1991, the boundaries of 16 territories were mapped by observing encounters of hooting males. Territory sizes ranged from 2.30-8.83 km², with an average of 4.83 ± 0.40 km².

A more direct comparison of space use between territorial and non-territorial owls consisted of a 3-week period in September 1990 and 1991 with locations for each night. Several measures of home range sizes are presented in table 2. Floaters had significantly larger 90 percent-areas (based on both mononuclear and multinuclear analysis); the multinuclear 70 percent-areas were not significantly different.

Reproductive Status of Non-territorial Owls

Floater movements and home ranges showed no consistent changes during courtship and egg-laying by territorial birds in February and March, as would be expected if male floaters sought extra-pair copulations or females settled on broods as secondary females. During 3 weeks of this fertile period for females in 1991 (see Rohner 1996), home range sizes were 7.72 ± 1.48 km² for the mononuclear 90 percent-area, 4.11 ± 2.16 km² for the multinuclear 90 percent-area, and 0.68 ± 0.15 km² for the multinuclear 70 percent-area. The daily movements were 1.309 ± 0.217 km vs 1.431 ± 0.124 km in the periods of September 1990 and 1991 ($p = 0.37$, Mann-Whitney $U = 12$, $n_1 = 5$, $n_2 = 7$).

Table 2.—Home range sizes of territorial and non-territorial Great Horned Owls (*Bubo virginianus*) during a 3-week period in September 1990 and 1991 at Kluane Lake, Yukon (one location per night, Rohner 1997). Sample sizes (a-b), three different measurements of home range size (c-e) are presented. Probabilities refer to the Mann-Whitney U-Test (two-sided).

Variable		Floaters	Territory owners	P
1990/91	(a) N owls	7	10	
	(b) N locations/owl	18.7 ± 1.0	20.0 ± 0	
mononuclear:	(c) 90%-area	7.25 ± 1.35 km ²	248.4 ± 41.4 km ²	0.002
multinuclear:	(d) 90%-area	4.68 ± 1.16 km ²	103.2 ± 15.9 km ²	0.011
	(e) 70%-area	0.56 ± 0.14 km ²	0.24 ± 0.04 km ²	n.s.



None of the birds settled on nests as secondary females of territorial males.

Territorial Behavior and Floaters

The home ranges of non-territorial owls overlapped broadly those of other owls of the same social class (fig. 3). On average, mononuclear 90 percent-areas overlapped by 23.3 ± 4.8 percent and multinuclear 90 percent-areas overlapped by 28.8 ± 6.4 percent ($n = 23$ overlappers and $n = 18$ over-lappers respectively, only for combinations of floaters that were monitored simultaneously and had > 1 percent overlap). There were no consistent differences between 1990 and 1991. Some overlapped with up to four other monitored floaters (fig. 3), and the highest overlap observed with one other floater was 87.8 percent (mononuclear 90 percent-area in 1991).

Floaters were not restricted to areas outside of established territories and intruded widely into several territories (all mononuclear 90 percent-ranges of figure 3 overlapped with at least five territories in the area of figure 4 where territorial boundaries were known). On a finer scale, however, some spatial segregation became apparent (fig. 4). Four of five floaters were

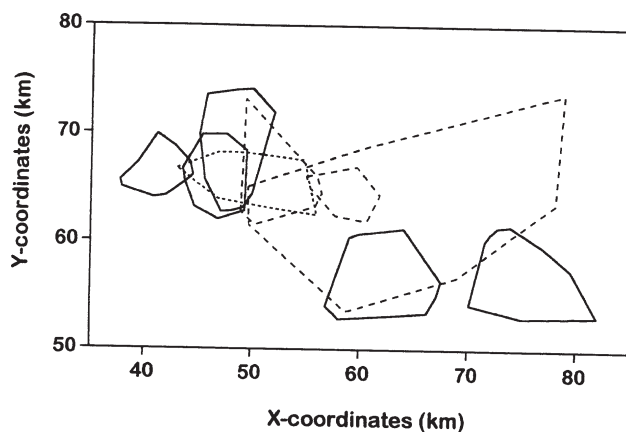


Figure 3.—Spatial overlap among non-territorial Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon (Rohner 1997). The home ranges presented are based on 90 percent-areas calculated by mononuclear clustering. Five owls monitored both in 1990 and in 1991 are identified by solid lines, one owl monitored only in 1990 by a broken line, and three owls monitored only in 1991 by dashed lines.

located significantly closer to territorial boundaries than expected from a random pattern (table 3). The median distance of random points to territorial boundaries was 0.343 km, the overall median of the results for individual floaters (not the median of the pooled data) was 0.229 km. This deviation of 33 percent was significantly different from random (bootstrap $P < 0.001$).

The hypothesis that territorial behavior limits population density can be tested by removal experiments (e.g., Newton 1992). While monitoring radio-marked Great Horned Owls, I observed six vacancies in territories which served as natural removal experiments (table 4). Territory holders either died or emigrated, and I recorded whether these vacancies were filled with new birds. In at least five of six vacancies, such replacements occurred. None of these owls were known territorial owls from the study area. In case two, it was unclear if the territory holder had been replaced or not. (Because it was often difficult to observe successful replacements, and because checks were made opportunistically, the dates when new territory holders were confirmed do not necessarily reflect the accurate time of replacement. The estimated intervals should therefore be considered upper limits of the real intervals.)

The hypothesis of social exclusion by territorial behavior was consistent with the result of density-dependent parameters in population growth. The number of established owl territories increased throughout 1988-1992 in response to a cyclic peak of snowshoe hares, but this yearly increase declined towards higher densities of pairs already present (fig. 5a). Although the sample size of only 4 years is small, the negative slope of the regression is significant ($y = 1.67 - 0.03x$, $r^2 = 0.95$, $p < 0.05$). As the number of established owl pairs increased and territories were packed more densely in the study area, not only the addition of further territories was reduced but also the floater pool increased strongly (fig. 5b, $y = 3.89x - 44.84$, $r^2 = 0.96$, $p < 0.05$; details in Rohner 1995).

Size of the Floater Population

The density of non-territorial floaters was estimated based on a population model including productivity, survival, and emigration (details in Rohner 1996). At peak hare densities, reproductive success and juvenile survival

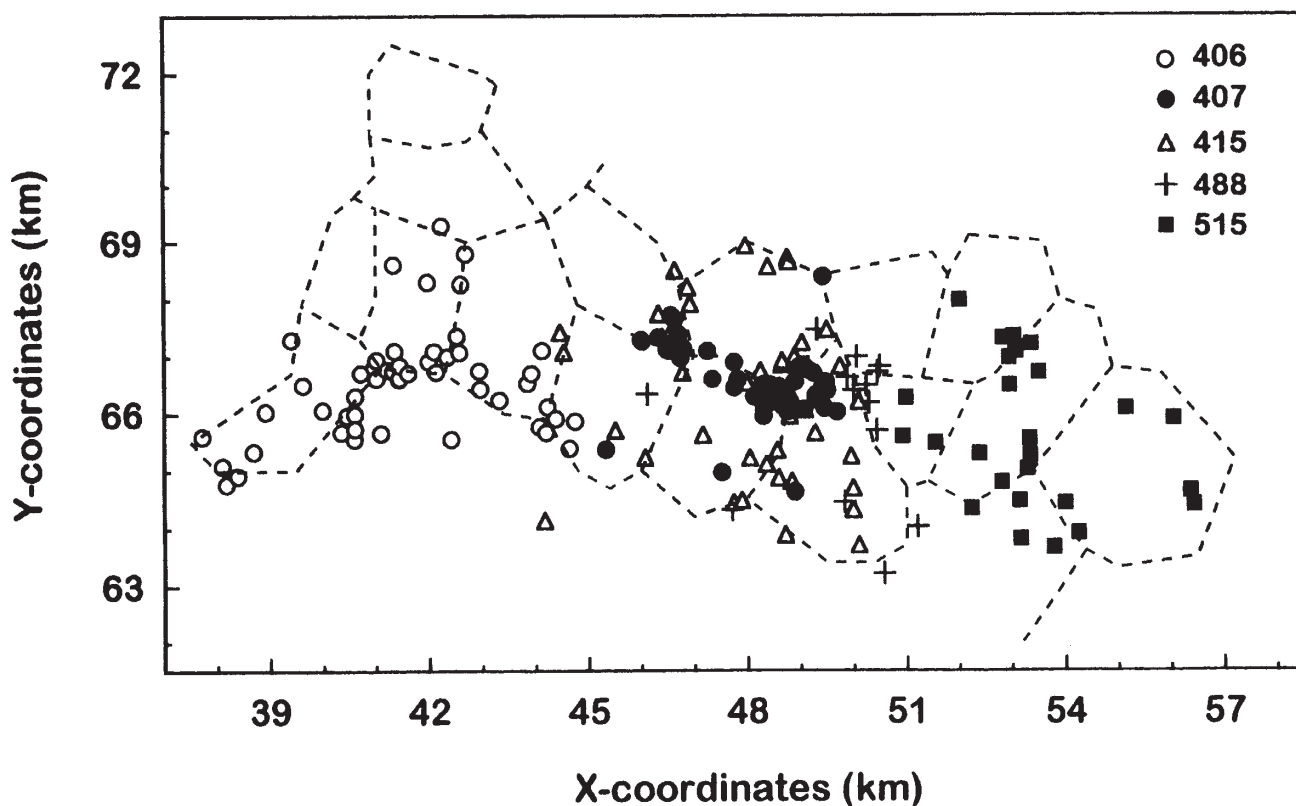


Figure 4.—Locations of Great Horned Owl (*Bubo virginianus*) floaters relative to territorial boundaries, during the period of September 1990 to June 1991 at Kluane Lake, Yukon (Rohner 1997). Five individual floaters (see table 3) are represented with different symbols and a total of 198 locations. All locations are shown within the minimum convex polygon that connects the outermost corners of these known territories. Less precise locations with 95 percent-error areas $<70.5 \text{ km}^2$ were excluded.

Table 3.—Distances of floater locations relative to the boundaries of territorial Great Horned Owls (*Bubo virginianus*) from September 1990 to June 1991 at Kluane Lake, Yukon (locations with 95 percent-error area $<0.5 \text{ km}^2$ and within the territories shown in fig. 6). For bootstrapping probabilities, the results from actual locations were compared to those from locations that were randomly distributed within the outermost boundaries of these territories (median distance of random points to territorial boundaries 0.343 km , quartiles $0.185\text{-}0.547 \text{ km}$).

N	Individual	Median (km)	Quartiles (km)	P
30	406	0.229	0.125-0.350	0.05
56	407	0.214	0.119-0.355	0.002
40	415	0.232	0.138-0.450	0.018
16	488	0.163	0.142-0.254	0.006
22	515	0.344	0.125-0.482	0.958
164	Pooled	0.222	0.130-0.381	<0.001



Table 4.—Natural removal experiments and replacements of radio-marked territorial Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon (Rohner 1996).

Sex	Estimated vacancy	Cause	Replacement confirmed	Interval to replacement
1. Female	10 Jul 1989	mortality	04 Dec 1990	ca. 4 months
2. Female	28 Jun 1991	mortality	-	?
3. Female	20 Nov 1991	mortality	12 Mar 1992	< 3.5 months
4. Male	25 Jan 1992	mortality	10 Mar 1992	< 7 weeks
5. Female	01 Feb 1992	emigration	12 Mar 1992	< 3 weeks
6. Female	26 Feb 1992	mortality	11 Mar 1992	< 6 weeks

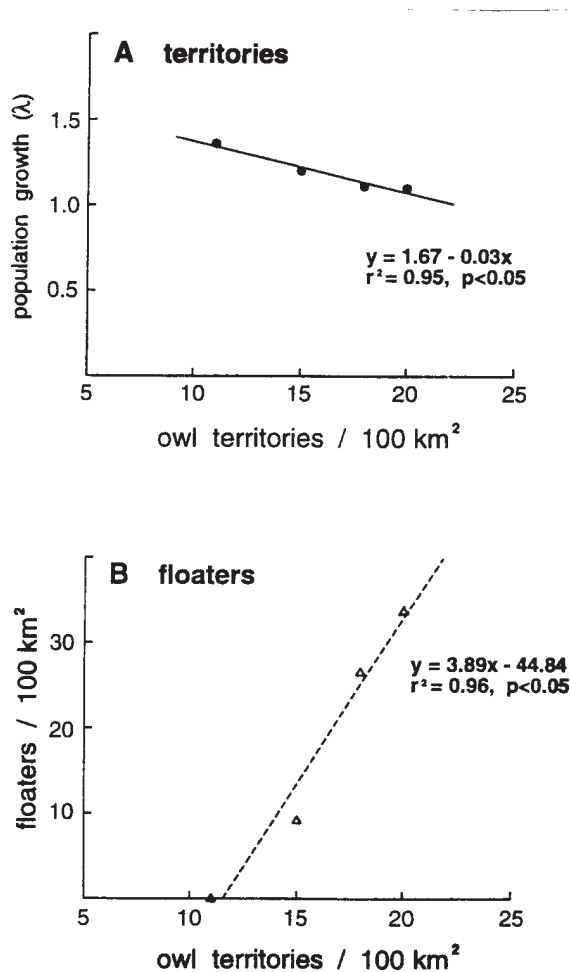


Figure 5.—Social behavior and the limitation of population growth in Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon (Rohner 1995). **A:** Growth rates of the territorial population decline as numbers of owl territories increase in the area (inverse density-dependent growth rate). **B:** Numbers of non-territorial 'floaters' increase as territories are packed more densely (density-dependent increase).

were very high (Rohner 1996, Rohner and Hunter 1996), therefore leading to large cohorts of dispersing juveniles in autumn. Weekly monitoring of radio-marked owls resulted in interesting differences in survival and emigration between floaters and territory owners (fig. 6). Survival was extremely high during the hare peak and emigration was negligible for both social classes. As the prey base declined, floaters were negatively affected before territorial birds (fig. 6). These differences were statistically significant (table 5).

The results of integrating these demographic parameters are presented in fig. 7a. Even when assuming that no floaters were present in spring 1988 for a minimum estimate, the numbers rose quickly from zero to densities similar to territorial owls (fig. 7b). The beginning of the hare decline in the winter of 1990/91 resulted in an immediate reduction in population growth due to emigration and lowered production of recruits by territorial pairs. Floater densities reached a peak with a time lag of 1 year relative to the hare cycle, and then dropped sharply from 1991 onwards, because of increased emigration and mortality, and because no additional juveniles were produced locally that could have compensated for losses in the non-territorial segment of the population.

The number of territorial owls in the study area increased almost linearly from 1988-1992 (fig. 7b, census data). Even when the hare population started to decline in 1990/91, the number of owl territories kept rising until spring 1992. Then, with a time lag of 2 years relative to the hare cycle, the number of territories dropped in 1993.

The numerical response of the total population of Great Horned Owls is given in figure 7b.

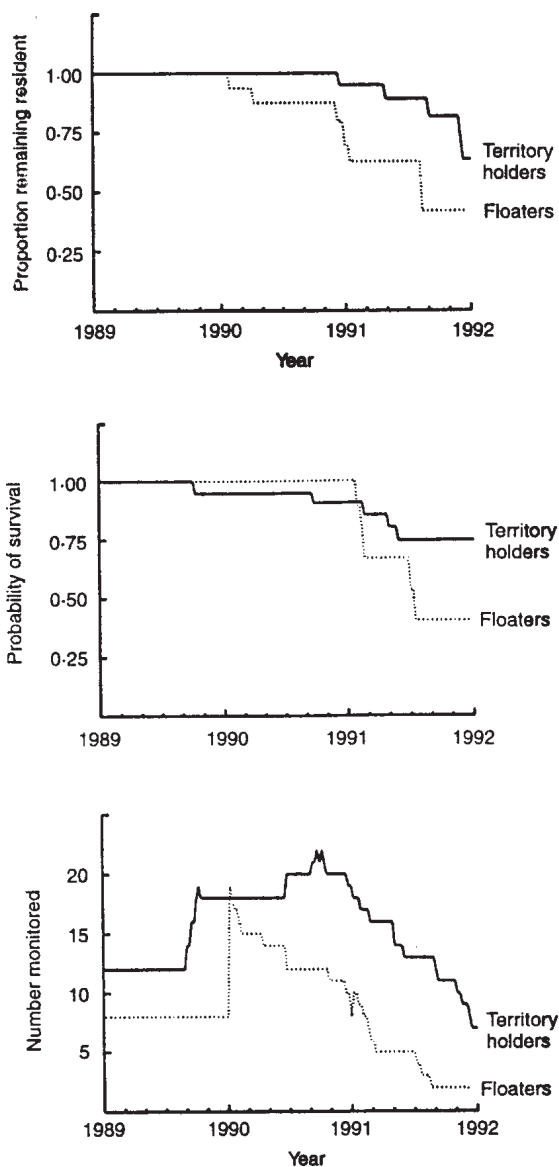


Figure 6.—Survivorship and emigration of adult Great Horned Owls (*Bubo virginianus*) (territory holders) and young owls (first and second year, floaters) based on radio-telemetry at Kluane Lake, Yukon (Rohner 1996). **A:** 'Residency rate' (1 meaning all owls remain resident, 0 meaning all owls emigrate). **B:** Probability of survival; **C:** Number of owls monitored. Years begin and end in early October.

Since the territorial segment represented a nearly linear component, the sum of densities or overall pattern more closely resembled the floater response with (a) an immediate reduction in population growth as hare densities declined, and (b) with a decline that was delayed by 1 year relative to the hare cycle.

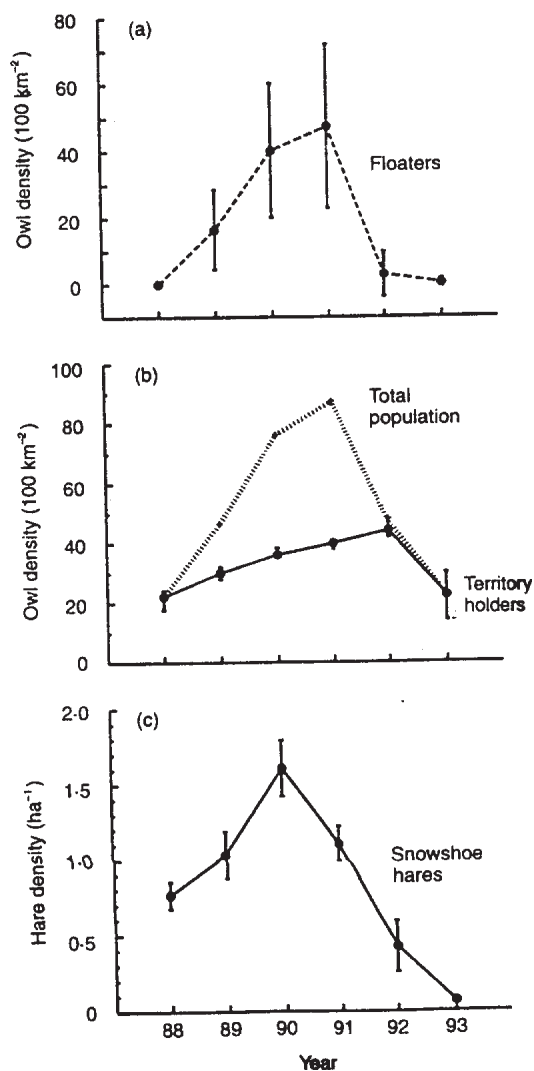


Figure 7.—Numerical response of Great Horned Owls (*Bubo virginianus*) (spring densities) to the snowshoe hare cycle at Kluane Lake, Yukon (Rohner 1996). **A:** Estimated density of non-territorial owls ('floaters'). **B:** Census of the territorial population (with minimum and maximum estimates), and total population (sum of territorial and non-territorial owls).

DISCUSSION

How Do Floaters Live in a Territorial Owl Population?

Non-territorial Great Horned Owls were not transient floaters that occurred at specific sites for only short periods of time. They used fairly stable home ranges with a space use similar to that of territorial Great Horned Owls. The most striking difference was in home range size.



Table 5.—Survival and emigration of Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon, as determined by radio-telemetry from fall 1989 to fall 1992 (Rohner 1995). Given are yearly survival rates (s_{Ti} and s_{Fi}), and yearly 'residency rates' (e_{Ti} and e_{Fi}), for territorial owls and floaters. Survival rates are (1-mortality), residency rates are (1-emigration). All rates (including overall calculations) are annual rates.

Time period	Hare densities	Social class	Survival \pm SE	Residency \pm SE	N monitored total (weekly avg.)
1989-1990	peak	territorial	.947 \pm .051	1.000	19 (14)
		floater	1.000	1.000	8 (8)
1990-1991	1st yr decline	territorial	.955 \pm .047	.950 \pm .049 ¹	22 (19)
		floater	1.000	.696 \pm .136 ^{1,2}	19 (13)
1991-1992	2nd yr decline	territorial	.819 \pm .132 ¹	.668 \pm .136 ²	18 (13)
		floater	.400 \pm .219 ^{1,2}	.600 \pm .268	10 (4)
1989-1992	overall	territorial	.905 \pm .073	.860 \pm .136	22 (16)
		floater	.701 \pm .174	.748 \pm .225	19 (8)

¹ $p < 0.05$ for difference between social classes (within individual years).

² $p < 0.05$ for difference to previous year (within social classes).

Based on weekly locations per year, floaters covered an area roughly five times the size of an average owl territory. Although floaters left more frequently for long-distance excursions and therefore were more flexible in seeking out opportunities, they shifted home range centers only 2-5 times more than territory owners. Much of this difference may be explained by the larger home ranges of floaters and an initially unstable phase when young floaters settle. Non-territorial Great Horned Owls were certainly not nomads using resources entirely opportunistically and free of spatial attachment (see also Rohner and Krebs 1997).

Why are floaters not more nomadic? One explanation may lie in the evolutionary design of forest owls (Martin 1986, Norberg 1987). Spatial knowledge may be paramount to hunting success in a highly structured habitat, particularly when information is incomplete in the dark, and may lead to conservative use of space ('nocturnal syndrome', Martin 1990; see also Rohner and Krebs 1996, Stamps 1995). An optimal hunting strategy may minimize space use, but floaters could be forced to use larger home ranges and choose hunting sites more opportunistically, simply because some of these sites are unavailable when occupied by territory owners. How familiarity with an area affects hunting success and mate acquisition remains to be studied.

Little is known how social behavior affects non-territorial owls, and the information available is usually restricted to evidence for the presence of non-territorial floaters (Austing and Holt 1966, Franklin 1992, Hirons 1985). Floating owls in our study were extremely secretive. They were never observed to vocalize and did not respond to playback of territorial calls. Floaters overlapped in their space use with each other, and seemed to move independently of each other. They did not concentrate in areas separate from territory holders but overlapped broadly with the occupied territories in the study area. At a finer scale, nevertheless, they were located more frequently along territorial boundaries than expected by chance. To my knowledge, this is the first direct evidence that territorial behavior can restrict the space use by floaters in owls.

Details of how non-territorial owls hunt in defended territories or how frequently they interact with owners aggressively, are unknown. In the study area, we found four Great Horned Owls that may have been killed by other Great Horned Owls. On one of those carcasses, a Great Horned Owl was seen, and owl footprints in the snow were observed at a second (F. Doyle, pers. comm.). Fatal fighting can evolve when a major part of a contestant's lifetime reproductive success is at stake (Enquist and Leimar 1990). This, for example,

may occur in saturated populations of Golden Eagles (*Aquila chrysaetos*) (Haller 1996). Many diurnal raptors have conspicuous immature plumages (Newton 1979) and display this bright coloration to approaching territory owners (Jenny 1992, pers. comm.). Such ritualized encounters may be more difficult in the dark, and it would be interesting to know the cost of being detected for an intruding floater, and which behavioral mechanisms floaters may use to reduce the risk of detection and injury. Although much work has confirmed that territorial males recognize the songs of their neighbors (e.g., Falls 1982), little attention has been paid to the possibility that non-territorial birds may use mental maps of territory boundaries plus the identification of the spatial distribution of singing males to assess their risk of detection when intruding into a territory.

Why Not Defend a Territory?

Is delayed maturation in owls an evolutionary strategy with higher fitness than breeding early? The results of this study do not support this hypothesis (see also Smith and Arcese 1989, Stearns 1992). Although very few young birds settled in territories during the first 2 years of their life despite peak populations of prey, three of the monitored owls proved that Great Horned Owls are capable of reproducing at the end of their first year of life. Large owls of the genus *Bubo* (L.) and *Nyctea* (L.) are known to breed as yearlings in captivity (Flieg and Meppiel 1972, K. McKeever, pers. comm.), but the age at first breeding in natural populations has only been speculated on (Adamcik *et al.* 1978, Henny 1972, Weller 1965). My observations of Great Horned Owls breeding as yearlings are the first to my knowledge. All of these birds were females. Earlier onset of breeding in females than males may represent a typical pattern, because both in owls and other raptors males establishing new territories are the sole providers of food for the female and the young throughout most of the breeding period, which may be more difficult than joining a male in a new territory and laying and incubating eggs (Newton 1979).

Is floating an alternative strategy with higher fitness because of opportunities for reproduction without the cost of territorial defense? Non-territorial females could attempt to breed as secondary females once the primary female is incubating (Korpimäki 1988). Although I

spent considerable effort attempting to document such cases, polygyny was never discovered, even during such extreme prey densities. Incubating females left their nests on several occasions to join hooting males at the territorial boundary, and I propose that territorial females prevent other females from settling. Such sex-specific defense has been demonstrated for Magpies (*Pica pica*), another species where long-term territories are occupied by a monogamous pair (Baeyens 1981).

Reproductive activity is more difficult to demonstrate for male floaters. There was no obvious change in movement patterns of floaters during the fertile period of females, suggesting that floater males did not become 'satellites' of territorial pairs in pursuit of opportunities for extra-pair copulations (Møller 1987). This, however, does not rule out that floater males reproduced. Floaters overlapped with territories, and an observation in Flammulated Owls (*Otus flammeolus*) showed that an extra-pair copulation can occur within a short duration and without any prior vocalizations (Reynolds and Linkhart 1990). Evidence for extra-pair copulations, however, has yet to be shown by further studies involving DNA analysis. Extra-pair paternity may be rare in diurnal raptors (review in Korpimäki *et al.* 1996), whereas the situation is basically unknown for owls. First results for Tengmalm's Owls (*Aegolius funereus*) (E. Korpimäki *et al.*, unpubl. data) suggest that extra-pair fertilizations may also be rare in strigiforms.

There is increasing evidence that territorial behavior can restrict the breeding activities and the establishment of territories in birds, and therefore can limit population growth (review in Newton 1992). In several bird species, aggressive encounters between territory holders and intruders, or the presence of non-breeding flocks have been noted. There is little evidence, however, for an effect of territorial behavior on the distribution of floaters particularly in forests (e.g., Arcese 1987, Matthysen 1989). The fact that floaters were located more often at the periphery of established territories does not prove that territoriality excluded these floaters from breeding (Watson and Moss 1970). Nevertheless, all results of this study including the presence of non-territorial birds capable of reproduction, replacements of territorial vacancies, reduced growth of the territorial population and accumulation of floaters as territories



became more packed, all support the hypothesis that territorial behavior excluded floaters from establishing territories and from breeding (see also Rohner 1995, Rohner and Smith 1996).

CONCLUSIONS

Floaters in Great Horned Owls were secretive and would not have been detected by standard censuses. During a cyclic peak of snowshoe hares, their numbers were estimated to reach 40-50 percent of the territorial, and therefore visible population. This raises some serious concerns for ecological and conservation approaches. For example, many studies have attempted to quantify the effect of predators on prey populations. In my case, the predation pressure on prey would have been severely underestimated if traditional censusing methods had been used. The notion of large floating populations may lead to a cautious interpretation of previous results, and may perhaps give incentives for expanded censusing techniques.

For conservation efforts, it is important to recognize territorial behavior as a dynamic component of populations. The age of floaters and their breeding potential are relevant to how natural populations respond to environmental change (Caughley 1977; Lande 1988; Newton 1991, 1992; Perrins 1991; Sinclair 1989). If floaters can breed, but are prevented from doing so by territory holders, they add flexibility to the dynamics of a territorial population. For example, the rapid increase of a population of Sparrowhawks (*Accipiter nisus* L.) recovering from high pesticide levels was possible because of high recruitment of young birds into the breeding segment of the population (Wyllie and Newton 1991).

This also raises a serious concern for conservation. When, as here, floaters are more affected by decreasing habitat quality than territorial birds, traditional monitoring programs that are based on censusing territories will not reveal these declines at an early stage (Wilcove and Terborgh 1984). In a scenario for slowly declining Spotted Owl populations, Franklin (1992) estimated that declines in territorial owls could not be detected for 15 or more years when floaters were present even at low densities.

Little is known about the size and structure of floater populations (Matthysen 1989, Newton 1992, Smith 1978, Smith and Arcese 1989). At

present, it is unclear to what degree these results also apply to non-cyclic owl populations. Further research on the mysterious life of non-territorial owls is strongly encouraged.

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