Have Lesser Scaup, *Aythya affinis*, Reproductive Rates Declined in Parkland Manitoba?

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Long-term surveys indicate that the scaup populations have declined over the past 20 years, and that this is probably the result of decreases in Lesser Scaup (*Aythya affinis*) rather than Greater Scaup (*Aythya marila*) numbers. To identify factors possibly related to the decline, we estimated demographic parameters for a local population of Lesser Scaup at Erickson, Manitoba, that was well studied before declines occurred and compared these estimates to historic rates. On average, nests were initiated later than in the past, and recent estimates of nesting success and duckling survival were lower than historical estimates. Breeding-season survival of adult females was estimated as 72.6%, with most (83%) mortality occurring during nesting. Current estimates of demographic rates at Erickson are too low to maintain a stable local population, and suppressed reproductive rates might be the proximate cause of the local population decline.

Key Words: Lesser Scaup, *Aythya affinis*, demographic parameters, duckling survival, female survival, life history, nesting success, Manitoba.

North American scaup numbers have been declining for over 20 years (Afton and Anderson 2001), and, in recent years, numbers have approached record lows (Garrettson et al. 2003). The decline in scaup numbers is more likely related to decreases in Lesser Scaup (*Aythya affinis*) rather than Greater Scaup (*Aythya marila*) [Afton and Anderson 2001]. While the majority of declines have taken place in the boreal forest where 68% of scaup breed, numbers at historically important breeding locales in the prairie-parklands have declined as well (Austin et al. 1998; Afton and Anderson 2001; Koons and Rotella 2003).

Hypotheses proposed to explain Lesser Scaup population decline (Austin et al. 2000; Afton and Anderson 2001) convey how possible changes in the environment have led to corresponding changes in demographic parameters (i.e., survival and reproductive rates) and thus, population size. However, despite our knowledge of some aspects of the life history of Lesser Scaup (Austin et al. 1998), information is lacking on potential changes in demographic parameters over the past 20 years, and environmental factors affecting demographic parameters. Specifically, few estimates of survival and reproductive parameters have ever been published for Lesser Scaup (see Austin et al. 1998), and there are only five published estimates from data collected during the past 20 years (Dawson and Clark 1996, 2000; Fournier and Hines 2001; Koons and Rotella 2003; Rotella et al. 2003).

A complete set of demographic parameters was estimated for Lesser Scaup on only one study area near Erickson, Manitoba (Afton 1984; Rotella et al. 2003) prior to the decline of the continental population. Estimates of demographic rates for Erickson scaup came primarily from Afton (1984) along with a few additional estimates (Rogers 1964; Hammell 1973; Rotella et al. 2003). Furthermore, using simple linear regression Koons (unpublished data) found that numbers of scaup detected on survey strata (Stratum 40; transect 6, segments 3 and 4; transect 4, segment 4 [raw data collected by the U.S. Fish and Wildlife Service, Laurel, Maryland, USA]) near Erickson were stable from 1970 to 1981 ($\beta = 7.2$; SE = 11.5; p = 0.55) but declined from 1982 to 2002 ($\beta = -16.5$; SE = 6.7; p = 0.02). We took advantage of information on Lesser Scaup at Erickson and conducted a study with the objectives of (1) estimating demographic parameters and comparing them with those estimated prior to the local population decline, and (2) evaluating relationships between demographic parameters and attributes of individual birds and environmental covariates.

Study Area

We conducted work on a 28.5-km^2 site (including the site used by Rogers [1964], Hammell [1973], Afton [1984], and Austin and Frederickson [1986]) located 4.8 km south of Erickson, Manitoba (50° 30'N, 99° 55'W) on the Riding Mountain Plateau in the parkland region. Land cover consisted of numerous small wetlands (12-19 wetlands/km^2), and patches of aspen (*Populus tremuloides* and *Populus balsamifera* [comprising 12% of the landscape]), within a landscape dominated by cereal grain agriculture (42%), grassland and pasture (17%), and hayland (15% [data acquired from analysis of 1994 black-and-white aerial photographs]).

Field Methods

Trapping and Telemetry

We trapped, radiomarked, and followed females during 15 May – 1 September in 1999 and 2000. We used decoy traps to capture some females each spring before they initiated nests. Each decoy trap contained a live captive-reared female scaup (Anderson et al. 1980) or a plastic decoy and mirrors. Nests of unmarked females were located using systematic foot searches, a chain drag (Klett et al. 1986), a rope drag, observations of females in or near nesting cover, or combinations of these methods. At nests that survived past five days of incubation, we trapped females using Weller nest traps (Weller 1957). For each female trapped, we recorded body mass (± 5 g), and estimated age using eye color (Trauger 1974). We outfitted each female with a 9-g prong-and-suture radio transmitter containing a 12-hr motion-mortality switch (Advanced Telemetry Systems, Isanti, Minnesota, USA) and a U.S. Fish and Wildlife Service aluminum leg band. Each female also was outfitted with a unique combination (color and shape) of nylon nasal disks (Lokemoen and Sharp 1985). Nest-trapped birds were anesthetized with propofol after handling to reduce nest abandonment (Machin and Caulkett 1998). Birds were released at the place of capture within 20 min of being removed from a trap. We then monitored radiomarked females throughout the breeding season with hand-held antennas, and truck-mounted or airplane-mounted null-peak antenna systems. Several times each week, we estimated each female's location and monitored survival status.

Nesting Success

Nests of non-radiomarked females were visited every 4 to 6 days to determine fate (Bart and Robson 1982). For nests of radiomarked females, we used female locations to monitor nest status. If a radiomarked female was not located at her nest for ≥ 24 hr, we checked the nest to determine its status. We defined a successful nest as one that hatched at least one egg (Klett et al. 1986). We recorded total clutch size at each nest that survived to incubation. Because full clutch size could not be accurately determined for three nests that were parasitized by Redheads (*Aythya americana*, [Sayler 1985]) or two nests found after a flooding event, we excluded these nests from clutch-size analyses. We also excluded the one known re-nest of a radiomarked female from the clutch-size analysis because Afton (1984) excluded re-nests.

Duckling Survival

To estimate duckling survival, we followed marked females that hatched nests, and we attempted to count the number of ducklings in each brood every 2 days until all ducklings in the brood died or reached 28 days of age. We used 28 days as an endpoint because duckling mortality is uncommon in ducklings > 4 weeks of age (Afton 1984; Dawson and Clark 1996). Whenever we suspected that a female had lost her brood, we repeatedly watched the wetland(s) being used by that female and radiotracked her intensively for a week. We concluded that a female had lost her brood if she was never seen with ducklings during that week. If a brood was not readily visible during a brood count, we made noise from a distance, which usually caused the brood to swim to the middle of the pond. Only two ponds on the study area had > 1 scaup brood on them, and duckling age was notably different among these broods. Still, to alleviate possible bias associated with brood mixing, we verified that the size and feather development of each duckling in a brood was consistent with the known age of that female's brood (Gollop and Marshall 1954).

Data Analyses

Nesting Success

To estimate scaup nesting success and to evaluate factors related to nesting success, we used data on nest fates (survived or died) for intervals of varying lengths (4- to 6-day intervals for non-radiomarked females, 1-day interval for radiomarked females). Because Afton's (1984) historic estimate of nesting success on our study area did not include data from island nests, we excluded three island nests. We evaluated factors potentially related to nesting success using generalized linear models (McCullogh and Nelder 1989) that employed a binomial distribution of errors for fate and a log-link function, and estimated potential observer-effects (Rotella et al. 2000) as well as regression coefficients for covariates of interest. This is a simple extension of the commonly used maximum likelihood estimator of Mayfield's daily survival rate (DSR) (Mayfield 1975; Johnson 1979; Bart and Robson 1982), which makes the same assumptions but allows one to examine the effect of visiting the nest on DSR.

We developed a simple a priori list of candidate models and considered each of the following covariates to be potentially related to DSR of nests: habitat type (upland or over-water nesting site), observer-effect (the effect of investigators visiting the nest), year, and period of nesting season. Because of the sparse data set, we could not consider calendar date as a continuous covariate, but had to group the survival intervals into three periods of the nesting season (early [12 June to 2 July], middle [3 July to 24 July], and late [25 July to 15 August]). According to guidelines provided by Burnham and Anderson (1998), the complexity of our model list was constrained by the amount of data available. Thus, we only considered univariate effects in our models. Support for each model was evaluated with Akaike's Information Criterion adjusted for sample size (AIC_c) and Akaike weights (Akaike 1973; Burnham and Anderson 1998:

51, 124). We considered the best approximating model to be that with the lowest AIC_c value and highest Akaike weight.

Because modeling was done on a log-transformed response variable, we estimated DSR and its confidence limits by back-transforming the regression equation and using an interval length of 1 day (Rotella et al. 2000). Each slope parameter (β_i) that appeared in the best approximating models was assessed based on the extent to which 95% confidence intervals for $\hat{\beta}_i s$ overlapped zero (Graybill and Iyer 1994).

Duckling Survival

We defined duckling survival as the proportion of all ducklings that survived from hatch to 28 days of age and brood survival as the proportion of broods that had at least one duckling survive for 28 days. Because some females abandoned their broods before 28 days of age, we used right-censored data (White and Burnham 1999); thus, brood survival estimates were not integer values. We assumed that brood amalgamation did not occur because we never saw a brood size increase and the age of each duckling was consistent with the age of the brood. To estimate duckling survival, we used a generalized linear model with binomial distribution of errors for fate and a logit-link function (McCullogh and Nelder 1989) and estimated the standard error by treating broods as clusters in a cluster sampling design (Flint et al. 1995). Because the sample of broods was too small to warrant comparison of competing models (see Results), we pooled yearly data and did not evaluate relationships between duckling survival and ecological covariates.

Female Survival

We used telemetry data (sequences of 1- to 6-day intervals collected throughout each field season), generalized linear models (McCullogh and Nelder 1989), and model-selection methods described above to estimate DSR for adult female scaup. Models estimated DSR for three periods: (1) non-maternal (DSR_{nm}, days spent on the study area when a female was not nesting or rearing a brood), (2) nesting (DSR_n), and (3) brood rearing (DSR_{br}). Period-specific estimates of DSR were then used to estimate the average breeding-season survival ($\hat{BS}$) of the local population with the following equation:

$$\hat{BS} = \hat{NB}\cdot(\hat{DSR}_{nm}^{\hat{d}nm}) + \hat{FN}\cdot(\hat{DSR}_{nm}^{\hat{d}nm})\cdot(\hat{DSR}_{n}^{\hat{d}n}) + \hat{SN}\cdot(\hat{DSR}_{nm}^{\hat{d}nm})\cdot(\hat{DSR}_{n}^{\hat{d}n})\cdot(\hat{DSR}_{br}^{\hat{d}br}),$$

where $\hat{NB}$ is the estimated proportion of females that were non-breeders; $\hat{FN}$ is the estimated proportion of females that attempted to nest but failed on all attempts; $\hat{SN}$ is the estimated proportion of females that attempted to nest and succeeded; and $\hat{d}_{nm}$, $\hat{d}_n$, $\hat{d}_{br}$, and are the mean number of days spent in each of the three periods, respectively. We used Afton's (1984) four-year average of 0.157 to estimate $\hat{NB}$ because our data were inadequate for estimating this parameter. Our telemetry data were used to estimate the remaining parameters.

Results

We captured and radio-marked 34 females ($n = 18$ in 1999, $n = 16$ in 2000). Of these females, six were trapped during the pre-nesting period and five of these were known to nest (one left the study area before nesting could be confirmed). Of these six females, three were one year old, two were two years old, and one was ≥ four years old. Of all females caught (not including re-sights of marked females), 10 were one year old, 16 were two years old, one was three years old, and seven were ≥ four years old. This sample provided data for 34 nests (including one known re-nest), nine broods, and female survival. We found 22 additional nests, and thus, located a total of 56 scaup nests, 49 of which provided data for estimating nesting success (seven nests were abandoned after the first nest visit). Fifty-seven percent of Lesser Scaup nests were located over water up to 1 m deep. Average nest-initiation dates for 1999 ($n = 33$) and 2000 ($n = 21$) were 24 June (SE = 2 d, median = 25 June, range = 31 May – 10 July) and 25 June (SE = 2 d, median = 26 June, range = 11 June – 20 July), respectively. Estimates of mean clutch size were 9.9 ($n = 26$, SE = 0.33, 95% CI = 9.3 to 10.6, range = 4 – 12) and 9.4 ($n = 13$, SE = 0.31, 95% CI = 8.8 to 10.0, range = 7 – 11) in 1999 and 2000, respectively.

Nesting Success

Our visits to 49 scaup nests created 288 intervals that ranged from 1 to 6 days in length. Estimated DSR was 0.940 (95% CI = 0.913 to 0.967) in 1999 and 0.943 (95% CI = 0.910 to 0.976) in 2000. Corresponding maximum-likelihood estimates of nesting success were 10.8% and 12.1%, respectively.

The best approximating model of DSR contained no observer, environmental, or year effects. This null model estimated DSR as 0.941 (95% CI = 0.921 to 0.962, 11.2% nesting success). The "period of nesting season" and "habitat type" models had ΔAIC_c values < 2.0, but these parameters were imprecise and had 95% confidence intervals that included zero.

Duckling Survival

Over two years, eight different radiomarked females hatched a total of nine broods and 54 ducklings (one female studied in both years; four broods in 1999 and five in 2000). The estimated 28-day duckling survival rate was 0.20 (95% CI = 0.00 to 0.58), and estimated brood survival rate was 0.48 (95% CI = 0.19 to 0.79).

Female Survival

We recorded no deaths during the non-maternal period ($n = 25$ females, 943 observation days). Given that our estimated DSR for the non-maternal period was 1.0, we checked if confidence intervals for estimated DSR in other periods included 1.00 and whether DSRs differed between the nesting (five mortalities) and brood-rearing (one mortality) periods. A model that estimated a common survival rate for nesting and brood-rearing ($n = 29$ females, 411 observation days; estimated DSR = 0.986, 95% CI = 0.975 to 0.997) periods was better ($\Delta AIC_c = 0.00$) than a model that generated period-specific estimates ($\Delta AIC_c = 1.34$). We estimated that 74.9% of radiomarked females attempted to nest but failed in all attempts, and 9.4% hatched young. The average number of days that a female was observed was 82, and average numbers of days spent in the nesting and brood-rearing periods were 26 and 19, respectively. We then incorporated these estimates into the breeding-season survival equation:

$$\hat{BS} = 0.157\cdot(1.00^{82}) + 0.749\cdot(1.00^{56})\cdot(0.986^{26}) + 0.094\cdot(1.00^{37})\cdot(0.986^{26})\cdot(0.986^{19})$$

The weighted product estimate of breeding-season survival produced by the model that pooled nesting and brood-rearing periods was 0.726 (95% CI = 0.575 to 0.932). By excluding the non-breeding component of the population, we estimated that the breeding-season survival for the component that attempted to breed at least once was 0.675 (95% CI = 0.496 to 0.919).

Discussion

Nesting

Our data suggest that nesting success of Lesser Scaup was poor at Erickson in recent years and similar to that from a concurrent study in parkland Saskatchewan (0.03, 95% CI = 0.004 to 0.12 [Brook 2002]). Nesting success at both locations may be lower than average values for the parklands (0.295), prairies (0.373), and boreal forest (0.572) [see Austin et al. 1998]. Although our estimate of nesting success was imprecise, the point estimate was much lower than the mean estimate from 1977-1980 at Erickson (Table 1). Further study will be needed on larger samples of nests and potential covariates of nest survival to understand why nesting success is so low at Erickson, and why recent estimates from the western boreal forest of Canada (Fournier and Hines 2001; Brook 2002) were lower than historic estimates (Townsend 1966; citations in Austin et al. 1998). Additionally, future studies need to examine the prevalence of suppressed nesting success across the breeding range of Lesser Scaup (Afton and Anderson 2001). Given that nesting success is thought to play a major role in the population dynamics of duck species, a decline in nesting success could have large impacts on population dynamics (Johnson et al. 1992); however, reasons for suppressed nesting success are not known.

Evidence from broad-scale studies of a variety of duck species suggests that nesting success of parkland and prairie-nesting ducks declined between 1935 and 1990 (Beauchamp et al. 1996), while the amount of cultivated land, predator diversity, and predator abundance all increased (Sargeant et al. 1993). However, the amount of cultivated land near Erickson during our study was similar to that of the early 1970s (Hammell 1973), and we had limited ability to make inferences about factors related to nesting success. Interestingly, Lesser Scaup bred sympatrically with one of their closest phylogenetic relatives, the Ring-necked Duck (*Aythya collaris*) [Livezey 1996], at Erickson and both nested at similar times of the year in similar habitats (Koons and Rotella 2003). However, they did not appear to compete for breeding territories. Nevertheless, Ring-necked Duck nesting success at Erickson was 2.9 times higher than that of Lesser Scaup. Further, the local Ring-necked Duck population is increasing while the Lesser Scaup population is decreasing (Koons and Rotella 2003). Thus, local habitat conditions might be suitable for scaup nesting. We speculate that changes in either food quantity or quality away from the breeding grounds have negatively impacted scaup physiology and nutrient reserves (Afton and Anderson 2001, Anteau 2002), which could in turn affect reproductive behavior and success.

Then again, we did not find a difference in fecundity between time periods at Erickson. Our estimate of mean clutch size (9.7) was similar to the pre-1981 estimate of 9.8 (Hammell 1973, Afton 1984). However, our mean date of nest initiation was delayed by one week when compared to 1977-1980 (Table 1). If females are returning to the breeding grounds in poorer physical condition than in the past, as Afton and Anderson (2001) have hypothesized, then one consequence could be delayed breeding, which we observed. Dawson and Clark (2000) found a negative relationship between hatch date and recruitment probabilities of Lesser Scaup ducklings. Thus, delayed breeding has the potential to negatively affect scaup populations. Future studies should determine the occurrence, causes, and consequences of late nesting.

Duckling Survival

Our point-estimate of duckling survival (0.20) was less than one third of the estimated mean for 1977-1980 (Table 1). Such a change would have large negative impacts on population size. Our estimate of duckling survival rate is among the lowest ever reported for ducks nesting at northern latitudes (see Rotella and Ratti 1992; Grand and Flint 1996) and is lower than estimates for Lesser Scaup in the western boreal forest of Canada (0.61, Brook 2002) and parklands of Saskatchewan (0.38, Dawson and Clark 1996). Low duckling survival could be related to delayed nest initiation. In other duck species nesting in the mid-continent, later hatched ducklings have poorer survival (Rotella and Ratti 1992; Dzus and Clark 1998; Guyn and Clark 1999). One study suggests that this trend may not hold for scaup (see Dawson and Clark 1996), but these same authors found that recruitment declines with hatch date (Dawson and Clark 2000). The ultimate effect of hatch date on recruitment would negate its effect on duckling survival.

Alternatively, low duckling survival may be associated with possible changes in the predator community, food abundance, or the prolonged wet conditions

TABLE 1. Period-specific estimates of Lesser Scaup demographic parameters at Erickson, Manitoba.

	1970-1971[a]			1977-1980[b]			1999-2000[c]		
Parameter	n	$\bar{x}$	95% C.I.	n	$\bar{x}$	95% C.I.	n	$\bar{x}$	95% C.I.
Nest-initiation date				78	15 June	10 – 20 June	54	24 June	21 – 27 June
Clutch size	35	9.0	8.6 – 9.4	77	10.3	10.1 – 10.5	39	9.7	9.2 – 10.2
Nesting success				129	0.31[d]	0.23 – 0.39	49	0.11	0.05 – 0.25
Duckling survival				39	0.68	0.43 – 0.92	9	0.20	0.00 – 0.58

[a] – The weighted mean across years from Hammell's (1973) study.
[b] – The weighted means across years from Afton's (1984) study.
[c] – The weighted means across years from this study
[d] – Afton (1984) found most of his nests in the early laying stages (1-3 d of age) by observing females fly or swim to the nest (A. Afton, personal communication). Thus, his estimates of apparent nesting success should be comparable to ours based on estimation of daily survival rate but may be biased high to a minor extent. *Note*: Rogers (1964) and Hammell (1973) estimated nesting success, but their methods and estimators are not comparable to ours.

in the study area prior to and during our study. Specifically, prolonged wetness may have led to increased abundance of Mink, *Mustela vison,* which are known to prey upon ducklings (Arnold and Fritzell 1987).

Female Survival

This is the first study to provide a known-fate estimate of breeding-season survival of adult female scaup. Our estimate of local breeding-season survival (0.726) is the lowest reported estimate for any northern-latitude breeding duck (Ringleman and Longcore 1983; Cowardin et al. 1985; Kirby and Cowardin 1986; Dwyer and Baldassarre 1993; Petrie et al. 2000). If we exclude non-breeders, our estimate is even lower (0.675, see Results). Historic estimates of breeding-season survival do not exist at Erickson. However, from 1977 to 1981 the annual survival of adults and juveniles was 0.59 (SE = 0.06 [Rotella et al. 2003]). If breeding-season survival equaled our estimate during 1977 to 1981, then survival during the non-breeding season would have averaged 0.81. This estimate seems high considering the birds must survive about nine months, two migrations, hunting season, and harsh weather during the non-breeding season (Blums et al. 2002). Nevertheless, our estimate of breeding-season survival is statistically similar to that for scaup at St. Denis, Saskatchewan, during 1992 to 2001 (0.82, SE = 0.12 [Rotella et al. 2003]), and to that at Yellowknife, Northwest Territories, during 1999 and 2000 (42 d estimate = 0.80, SE = 0.09 [Brook 2002]). All estimates of female scaup mortality on the breeding grounds are high, which could have substantial effects on population growth rate (Koons 2001), and could be contributing to the declines of Lesser Scaup populations.

Our data indicate that survival was lower during maternal periods (nesting and brood-rearing) than during non-maternal periods, indicating that it is costly for a mother to attend to young. Further, almost all of the mortality (83%) occurred at nests. Because we found three dead female scaup in Mink dens and noted canine marks that matched those of Mink on all other dead females, we believe that Mink killed all six females. Similarly, Afton (1984) noted that seven marked females were killed on nests in 1979 and 1980 (Mink killed four and Red Fox [*Vulpes vulpes*] killed three). Future studies should examine the predator-prey interactions between Mink and scaup.

Study Limitations

Because of local population decline (see Introduction), the population of scaup that existed during our study was small and prevented us from achieving desired sample sizes. This limited our ability to detect environmental factors that might influence demographic rates. We acknowledge that our results for parameters estimated from radiomarked females would be biased low if transmitters negatively affected females or if a trapping bias existed. Across all demographic rates, we did not detect marker-effects nor did we detect a trapping bias across female age, body size, or mass (unpublished analyses). However, we must note that our sample sizes were too small to adequately test for such effects. Furthermore, we did not explicitly design our study to collect comparable data for birds with and without radios. Still, lightweight radio-transmitters, similar to ours, have been used on Lesser (Custer et al. 1996; Brook and Clark 2002) and Greater Scaup (P. L. Flint and J. B. Grand personal communication) without obvious effects. Furthermore, five out of six birds that were marked before the nesting season did nest (the other bird left the study area).

Conclusions

Our results indicate that the Erickson scaup population may be nesting later than in the past and presently has lower nesting success and duckling survival than in the past. Furthermore, adult female breeding-season survival was alarmingly low during our study. In general, these findings are consistent with the hypothesis that reproductive success has declined (Austin et al. 2000; Afton and Anderson 2001). Our estimates were not precise enough to allow us to conclude definitively that reproductive success has declined. Nevertheless, these demographic parameters may have been

at low levels during our study due to alteration of habitat on and off the breeding grounds, prolonged wet conditions on the study area and associated numerical responses by key predators, or all. Apart from three-year olds, the age structure of our captured population was approximately similar to that during Afton's study (1984). While age structure has strong potential to affect scaup demography (Afton 1984) and short-term population dynamics (Fox and Gurevitch 2000), we do not believe age structure was responsible for the low reproductive success of scaup in 1999 and 2000 at Erickson.

Assuming nesting success and breeding-season survival were low, and that most female mortality occurs at nests, it is likely that management aimed toward increasing the security of nests will benefit both nesting success and survival of females. Before such management action can be taken across large areas, demographic parameters of scaup populations need to be estimated across broader spatial and temporal scales to examine the ubiquity of our results. Data are especially needed for the boreal forest. Additionally, large samples of marked birds will be required to effectively examine ecological factors related to, and responsible for, variation in demographic parameters. Lastly, we suggest that future research address physiological and cross-seasonal factors related to Lesser Scaup breeding chronology and success to test other hypotheses and ultimate factors related to the decline in scaup numbers (Afton and Anderson 2001).

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Landscape Influence on *Canis* Morphological and Ecological Variation in a Coyote-Wolf *C. lupus* × *latrans* Hybrid Zone, Southeastern Ontario

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The ecology of Coyote-Wolf (*Canis latrans* × *C. lupus*) hybrids has never fully been typified. We studied morphological and ecological variation in *Canis* within a region of Coyote-Wolf hybridization in southeastern Ontario. We assessed *Canis* morphology from standard body measurements and ten skull measurements of adult specimens and found that *Canis* in this region are morphologically intermediate between Algonquin Provincial Park Wolves (*C. lupus lycaon*) and Coyotes, indicating a *latrans* × *lycaon* hybrid origin; however, there is a closer morphological affinity to *latrans* than *lycaon*. Analysis of 846 scats indicated dietary habits also intermediate between *lycaon* and Coyotes. We used a geographic information system (GIS) to assess spatial landscape features (road density, land cover and fragmentation) for six study sites representing three landscape types. We found noticeable variation in *Canis* morphology and diet in different landscape types. In general, canids from landscape type A (lowest road density, more total forest cover, less fragmentation) displayed more Wolf-like body morphology and consumed a greater proportion of larger prey (Beaver [*Castor canadensis*] and White-tailed Deer [*Odocoileus virginianus*]). In comparison, canids from landscape types B and C (higher road density and/or less total forest cover, more fragmentation) were generally more Coyote-like in body and skull morphology and made greater use of medium to small-sized prey (Groundhog [*Marmota monax*], Muskrat [*Ondatra zibethicus*] and lagomorphs). These landscape trends in *Canis* types suggest selection against Wolf-like traits in fragmented forests with high road density. The range of *lycaon* southeast of Algonquin Provincial Park appears to be limited primarily due to human access and consequent exploitation. We suggest that road density is the best landscape indicator of *Canis* types in this region of sympatric, hybridizing and unprotected *Canis* populations.

Key Words: Coyote, *Canis latrans*, Gray Wolf, *Canis lupus*, hybridization, road density, morphology, landscape influence, Ontario.

The objectives of this study were to assess potential relationships between landscape characteristics (e.g., road density, forest cover and fragmentation) and morphological and ecological variation in *Canis* in a Coyote-Wolf hybrid zone of southeastern Ontario. Coyote-Wolf (*Canis latrans* × *C. lupus*) hybridization (Lehman et al. 1991; Wilson et al. 1996) and intermediate-sized canids (Kolenosky and Standfield 1975; Nowak 1979; Schmitz and Kolenosky 1985; Schmitz and Lavigne 1987) have previously been described in eastern Ontario, an interface region between Wolf range in the north and Coyote range in the south (Kolenosky et al. 1978; Buss and de Almeida 1997). In parts of the Great Lakes region, spatial landscape features have been used to describe areas of favorable Wolf habitat (Thiel 1985; Jensen et al. 1986; Mech et al. 1988; Fuller et al. 1992; Mladenoff et al. 1995), but not in relation to Coyote-Wolf hybridization.

Habitat and landscape conditions have been implicated in the extirpation of wild Red Wolves (*C. rufus*) prior to 1970, the shrinkage of the range of *C. lupus lycaon* and coyote colonization in eastern North America (Nowak 1978; Moore and Parker 1992), as well as extensive *latrans-lycaon* and *latrans-rufus* hybridization (Lehman et al. 1991; Wayne and Jenks 1991; Roy et al. 1994). The study area on the Frontenac Axis of southeastern Ontario is characterized by a forested matrix ranging from landscapes of continuous forest and low road density, potentially suitable Wolf habitat (Thiel 1985; Jensen et al. 1986, Mech et al. 1988; Fuller et al. 1992; Mladenoff et al. 1995), to mixed forest-agricultural landscapes. It was hypothesized that *lycaon* would be found in continuously-forested landscapes similar to Algonquin Provincial Park to the north, and that Coyote-like animals would predominate in landscapes with less forest cover, more agricultural activity and higher road density.

This paper is relevant to the conservation of the adjacent Algonquin Provincial Park *lycaon* population. *Lycaon*, which has lost over half its historic range (Nowak 1995), is considered a subspecies of Gray Wolf (Nowak 1995), or more recently, a separate species, *C. lycaon*