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The effects of anthropogenic alteration of nesting habitat on rates of extra-pair fertilization and intraspecific brood parasitism in Canada Geese *Branta canadensis*

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Parentage studies have shown that alternative reproductive strategies are widespread in many avian taxa that were once thought to be monogamous. Recent anthropogenically mediated habitat change may have disrupted ecological factors, such as breeding density, which have given rise to inter- and intraspecific variation in the frequency of extra-pair fertilization (EPF) and intraspecific brood parasitism (IBP). We used genetic analyses to quantify the incidence of alternative reproductive strategies exhibited within clutches of Canada Geese *Branta canadensis maxima* nesting in high- and low-density situations in and around urban areas in southern Michigan, USA. We tested the hypothesis that high nesting density would increase the frequency of EPF and IBP. There were no significant differences in rates of EPF and IBP clutches (14 and 26% of clutches, respectively) from nests in high-density (21.7% EPF, 21.7% IBP) vs. low-density (5.3% EPF, 31.6% IBP) areas, although high-density sites had a fourfold higher rate of EPF. Rates of EPF and IBP in high-density urban areas in Michigan were comparable to rates observed in other species nesting under different ecological conditions. Levels of relatedness between host and parasitic females were higher than expected by chance, suggesting that related females are more tolerant of one another and that host females could gain inclusive fitness benefits from rearing parasitic offspring. Our study highlights the importance of understanding the different costs and benefits associated with alternative behavioural repertoires that may vary as habitats and associated selection pressures are increasingly modified by human activities.

Keywords: alternative reproductive tactics, anthropogenic habitat modification, *Branta canadensis maxima*, density-dependence, microsatellites, nesting density, urbanization.

Contrary to inferences from field studies (Lack 1968), paternity analyses using molecular techniques have revealed that very few avian mating systems are truly monogamous (Griffith *et al.* 2002) and hence that many bird species exhibit alternative reproductive strategies. For instance, among many 'socially monogamous' species, copulations regularly occur outside the primary pair, resulting in extra-pair fertilization (EPF) (Petrie & Kempenaers 1998, Griffith *et al.* 2002). The frequency of EPF varies considerably among populations and species, ranging from 0% (e.g. Great Northern Diver *Gavia immer*; Piper *et al.* 1997) to extreme cases where over 95% of clutches are the result of extra-pair copulations (e.g. Saltmarsh Sparrows *Ammodramus caudacutus*; Hill *et al.* 2010). Likewise, intraspecific brood parasitism

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(IBP), where a female lays eggs in the nest of a conspecific who subsequently provides all parental care, is now well documented (Yom-Tov 2001). However, the mechanisms underlying the extreme variation in the occurrence and frequency of alternative reproductive strategies are poorly understood.

Individuals can exhibit considerable plasticity in behavioural strategies in response to social and ecological factors. However, contradictory results from different studies have made it difficult to tease out conclusive patterns (Griffith *et al.* 2002). For instance, a positive relationship between density and the frequency of EPF has been found for American Robins *Turdus migratorius* (Rowe & Weatherhead 2007) and Barn Swallows *Hirundo rustica* (Møller 1991), whereas no relationship was found for Black-Throated Blue Warblers *Dendroica caerulescens* (Chuang *et al.* 1999), and a negative relationship between density and EPF was detected in Great Reed Warblers *Acrocephalus arundinaceus* (Leisler *et al.* 2000) and Tree Swallows *Tachycineta bicolor* (Conrad *et al.* 2001). The frequency of EPF is potentially dependent upon factors that affect mate encounter rates and the timing of extra-pair copulations relative to when the eggs are fertilized (Westneat & Stewart 2003, Stewart *et al.* 2010). Males are expected to participate in extra-pair copulations when male parental care is low, breeding density and female receptivity are high, and breeding synchrony and mate guarding are low (Westneat *et al.* 1990, Westneat & Sherman 1997, Shuster & Wade 2003). Females are expected to seek extra-pair copulations when they can select among mates, when male quality varies, and when social and ecological limitations are low (Gowaty 1996). Likewise, IBP is expected to occur in species with high fecundity, when nesting sites are limited, when breeding densities are high and when costs of parental care are reduced for parasitic females (Zink 2000, Yom-Tov 2001). Although these expectations are well supported, empirical studies investigating these relationships across taxa have often found contradictory results.

Anthropogenic habitat modifications can affect the plasticity of avian reproductive strategies by affecting population densities and nest-site availability. For instance, artificially increasing nest availability with the use of nestboxes has been shown to increase the frequency of IBP in Wood Ducks *Aix sponsa* (Semel *et al.* 1988). Furthermore, Semel *et al.* (1988) showed that nestboxes placed in habitats approximating natural conditions (i.e. more obscured by natural vegetation) were less likely to be parasitized than those in more open, artificial habitats and that high levels of IBP could lead to population crashes. The high visibility of nest-sites in modified habitats may predispose nests to increased rates of brood parasitism. However, species may respond differently to the same anthropogenic pressures simply because of underlying variation in natural behavioural repertoires. As anthropogenic habitat modification becomes increasingly prevalent, understanding the resultant variation in natural reproductive behaviours is necessary to assess the effects of habitat modification on reproductive success and population dynamics (de Valpine & Eadie 2008).

We investigated the frequency of alternative reproductive strategies in a wild population of Canada Geese *Branta canadensis maxima* in southern Michigan, USA, experiencing varying ecological conditions. Canada Geese are dispersed territorial nesters and are primarily socially monogamous with long-term pair bonding (Allan *et al.* 1995). Males and females provide extensive parental care (Ely 1989). In southern Michigan, the abundance and distribution of Canada Geese have increased dramatically since the 1970s. Geese often inhabit anthropogenically modified habitats at abnormally high densities, partly due to the increased resources available for brood foraging (Smith *et al.* 1999). In non-migratory populations, female Canada Geese are highly philopatric, increasing local levels of female relatedness over time. Females may be more tolerant of related conspecifics, which could also contribute to the high densities found in modified habitats (Kaminski & Prince 1977). Plasticity in nest-site choice enables females to nest in a variety of habitats and close to one another (nests can be < 2 m apart; Allan *et al.* 1995). If nest-sites are rarely limited by suitable habitat or by breeding density, the frequency of IBP could be low and unaffected by social conditions. Conversely, IBP rates could increase with higher density simply because more host nests are available. If breeding density affects the frequency of EPFs in Canada Geese, the rate might increase with density, as more females are available for males to pursue (Westneat & Stewart 2003).

Modified landscapes present opportunities to examine the effects of extreme variability in conspecific density on the frequency of alternative reproductive strategies and to tease apart the evolutionary and ecological factors affecting reproductive behaviour. Because expanding Canada Goose populations are now considered a nuisance by many residents of urban and suburban areas (Forbes 1993, Ankney 1996), understanding and documenting how reproductive strategies vary between high- and low-density populations may provide much needed information for management of urbanized geese and other avian species. Knowing how goose reproductive behaviour is affected by human land use and habitat alterations may enable managers to provide more effective guidelines for minimizing the growth of nuisance geese populations.

METHODS

We collected mother and offspring samples from 42 natural nests at 33 sites in Oakland, Wayne, Washtenaw, Livingston, Shiawasee, Ingham, Jackson and Eaton counties, Michigan (Fig. 1) over three breeding seasons (2000–2002). Each site was qualitatively categorized as high- or low-density. Low-density nests (n = 19) were all sampled from natural palustrine emergent or riverine marshes surrounded by intact upland forest. Sampled nests from low-density sites were mostly located on Muskrat O*ndatra zibethicus* mounds on the edges of these marshes, where crowding by conspecifics was not tolerated (Kaminski & Prince 1977). Nearest nesting neighbour distance for low-density sites was ≥ 100 m and foraging opportunities for broods were limited to the wetland. Nests from high-density sites (n = 23) were all located in urban and/or suburban parks, developments or office complexes where natural habitat features were limited or non-existent and planted grass and lawn predominated. Most high-density sites were located on small islands. Nearest nesting neighbour distances were ≤ 3 m (islands) and ≤ 20 m (non-island situations) for high-density sites. Natural marshes cannot support the abnormally high density of nests that occur in urban areas (Allan *et al.* 1995) or on islands (Zenner & LaGrange 1998). Smith *et al.* (1999) attribute this to the limited resources available for foraging broods, which strictly limits the number of breeding pairs that a site can support. Canada Geese nesting in urban environments are known to tolerate higher nesting densities and have higher gosling survival (Balkcom 2010), contributing to high population growth rates.

Blood was collected from the brachial vein/artery from nesting females and stored in Eppendorf tubes containing storage buffer (2% sodium dodecyl sulphate (SDS), 50 mM ethylenediaminetetraacetic acid (EDTA), 50 mM Tris; Longmire *et al.* 1997). Eggs representing entire clutches were removed from the corresponding nests (Michigan State University, Animal Use and Care permit AUF 01/03-002-00) and transferred to the lab, where embryonic tissue was extracted from unhatched eggs and stored in storage buffer (0.5% SDS, 100 mM EDTA, 100 mM Tris at pH 8.0, 10 mM NaCl). Nuclear DNA was extracted from the blood and tissue samples using the Gentra PureGene protocol (Gentra Systems, Minneapolis, MN, USA). The DNA was resuspended in TE (10 mM Tris–HCl, pH 8.0, 1 mM EDTA) and quantified, and 100 ng of DNA was used in each polymerase chain reaction (PCR).

PCR was conducted using four fluorescently labelled microsatellite DNA primers: Bcaμ9, Hhiμ1 (Buchholz *et al.* 1998), CR-G (A. Baker unpubl. data) and TTUCG5 (Cathey *et al.* 1998). PCR of each of the four loci involved 30 cycles of 1 min denaturation at 94 °C and 1 min annealing at 60 °C, 56 °C, 54 °C and 51 °C, followed by 1 min elongation at 72 °C (Pearce *et al.* 2000). Samples were loaded onto a 6% denaturing polyacrylamide gel with molecular weight standards and samples of known genotype. PCR products were scanned using a Hitachi FMBIO II instrument. All gels were scored independently by two experienced lab personnel. A random sample of 10% of all individuals was genotyped twice to ensure consistency of results and to screen for any errors. Concordance between the first and second runs was high (< 1% error).

Genotypes of all female adults were used to test loci for errors and examine population parameters. We used the program MICRO-CHECKER 2.2.3 (Van Oosterhout *et al.* 2004) to test for the presence of null alleles, stuttering or allelic dropout. We also tested for deviations from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD) using the program GENEPOP 4.0.1 (Raymond & Rousset 1995). We used a Monte Carlo chain method (1000 dememorizations, 100 batches, 1000 iterations) following the algorithm of Guo and Thompson (1992) and applied a Bonferroni correction for a table-wide significance level of 0.05.

The probability of identity (P_{id}), the probability that two unrelated individuals share the same

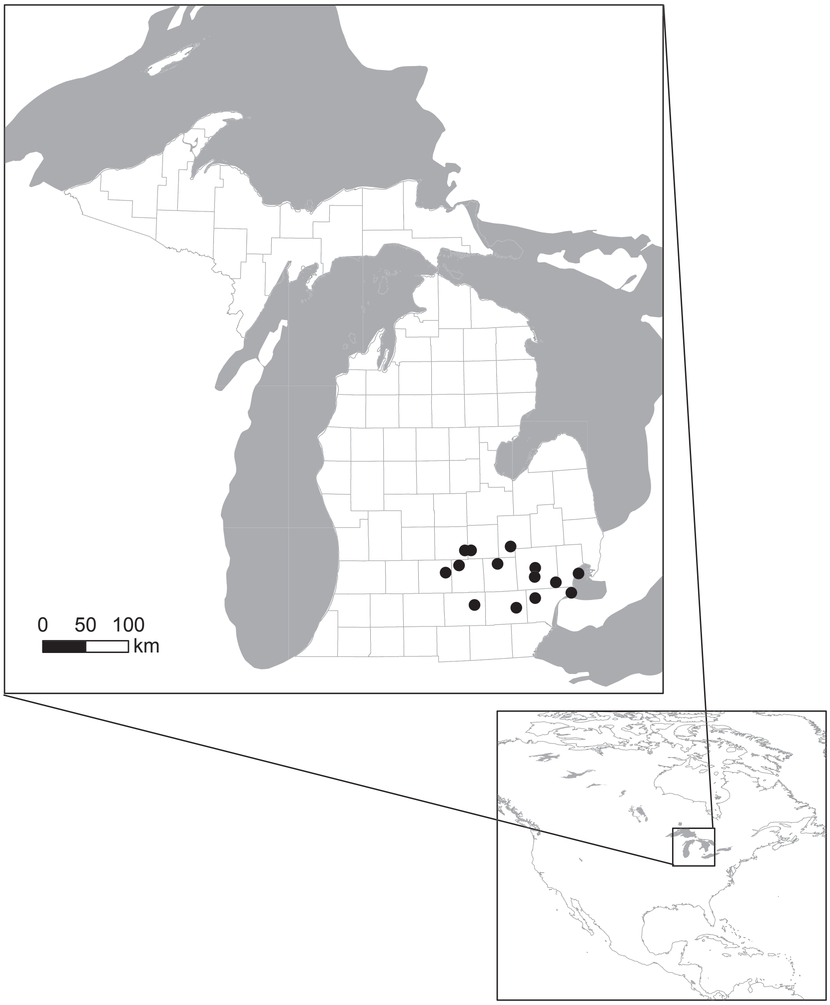

Figure 1. Map of Canada Goose sampling localities in southern Michigan, with county boundaries represented. Inset represents approximate sampling area within North America.

genotypes at a given locus, was calculated as described by Bruford *et al.* (1992). The probability of paternal exclusion (P_{ex}), the probability by which we could exclude an attending parent as a genetic parent of an offspring when in fact that parent was not the genetic parent, was calculated following Bruford *et al.* (1992). Allele frequencies used in these calculations were based on an independent sample of the population within southeast and south-central Michigan, in which the population was in HWE and loci were in linkage equilibrium (Scribner *et al.* 2003). We used the program GENECAP (Wilberg & Dreher 2004) to examine the data for identical genotypes and calculate the sibling probability of identity ($P_{(ID)sib}$) as described by Evett and Weir (1998). Sibling probability of identity is a conservative estimate that sets an upper bound for the probability of two individuals sharing identical genotypes in a population (Waits *et al.* 2001).

A nest was classified as IBP if one or more offspring genotypes did not match the known maternal genotype for at least one locus. Likewise, nests were classified as EPF if more than two paternal alleles were represented in all of the offspring for at least one locus. Based on four-locus genotypes, including the known maternal genotype, we used the program GERUD v. 2.0 (Jones 2005) to analyse clutches and identify maternal–offspring mismatches (indicative of IBP). We also used GERUD to identify cases of EPF, where more than two paternal alleles were present at any offspring locus within a clutch. GERUD uses a stepwise procedure to determine the minimum number of sires necessary to explain the progeny array associated with each maternal genotype. First, maternal alleles are subtracted. Paternal alleles are then combined to produce all possible multilocus genotypes. If one paternal genotype can explain the array, the clutch is identified as singly sired and putative paternal genotypes are retained. Mismatches identified by GERUD were further examined by eye to rule out any putative null alleles or mutations, which GERUD does not accommodate.

We examined levels of relatedness in the population and between mothers and their offspring. To determine the background population level relatedness, we calculated pairwise coefficients of relatedness (r_{xy}) between all females sampled in our study ($n = 42$) using the Queller and Goodnight mean estimator (Queller & Goodnight 1989) in GENALEX 6.3 (Peakall & Smouse 2006). In a randomly mating panmictic population, the hypothetical expectation is that the mean of pairwise relatedness values is zero. We also calculated r_{xy} of all mothers and their true offspring, and host females and their parasitic offspring resulting from IBP. We would expect that the r_{xy} values between mothers and their true offspring should be normally distributed around 0.5. We tested the difference in mean r_{xy} values between the host female–parasitic offspring pairs and the population mean. A higher than expected mean r_{xy} could indicate that the parasitic and host females are related. From the distribution of r_{xy} calculated as a baseline, using females only, we drew 10 000 random samples of $n = 26$ (equal to the number of actual pairwise comparisons between mothers and parasitic offspring). Significance was assessed as the proportion of times the random mean was greater than the actual mean.

To test the effects of density, clutch size and annual variation on the frequency of IBP and EPF, we conducted logistic regression analyses in R (R Development Core Team 2006). Response variables were presence/absence of IBP and EPF in individual clutches, and predictor variables (fixed effects) were density, year and number of offspring in a clutch. Significance of model parameters was inferred at $P < 0.05$.

RESULTS

We genotyped 253 individuals (211 offspring and 42 females) comprising 42 clutches (Table 1) collected over three breeding seasons (2000–02). There was no significant evidence of null alleles, allelic dropout or stuttering in our loci ($\alpha = 0.01$). Likewise, no loci showed significant deviations from HWE or LD, and thus all loci were retained for further analyses. Allelic diversity ranged from seven to 11 alleles per locus. Observed heterozygosity was high (range 0.659–0.841) across loci. Estimates of single locus probabilities of identity (P_{id}) ranged from 0.212 to 0.243 and over all loci $P_{\mathrm{id}} = 5.29 \times 10^{-5}$. The probability of exclusion (P_{ex}) ranged from 0.403 to 0.745 at single loci, with combined $P_{\mathrm{ex}} = 0.96$. All adult females had unique multilocus genotypes and $P_{\mathrm{(ID)sib}}$ was estimated to be 1.97×10^{-2}. Identical genotypes were found for some pairs of offspring, and most matching pairs (84% of matches, $n = 26$) were two offspring from the same clutch.

Of the 42 nests sampled, 25 (59.5%) had no detectable evidence of IBP or EPF. No maternal–offspring mismatches were present, and no more than two paternal alleles were identified in these clutches, consistent with inferred monogamy. Over all sites, six of the 42 clutches (14%) showed evidence for EPF. Furthermore, 11 of the 42 clutches (26%) showed evidence for IBP. Five of the six clutches designated as EPF were based on more than two paternal alleles being present at two or more loci. Likewise, seven of the 11 clutches that were designated as IBP were based on maternal mismatches at two or more loci.

Average pairwise relatedness for the population, based on adult females only, was $r_{xy} = -0.025$ (sd = 0.29, range = −0.76 to 0.89), conforming to the expectation of mean $r_{xy} = 0$ (Fig. 2). Likewise, coefficients of relatedness between mothers and their true offspring ($r_{xy} = 0.57$, sd = 0.16; range = 0.10–1.00) conformed to the expectation of $r_{xy} = 0.50$. Coefficients of relatedness between

Table 1. Summary of Canada Goose egg clutches sampled at low- and high-density sites during three breeding seasons (2000–2002) including sample size (*n*), the frequency of extra-pair fertilization (EPF) and intraspecific brood parasitism (IBP). The percentage of the total is in parentheses.

	High			Low		
Year	*n*	EPF	IBP	*n*	EPF	IBP
2000	11	3	3	5	1	1
2001	7	2	1	7	0	3
2002	5	0	1	7	0	2
Total	23	5 (21.7)	5 (21.7)	19	1 (5.3)	6 (31.6)

host mothers and their parasitic offspring (mean $r_{xy} = 0.15$, sd = 0.21; range = −0.28 to 0.56, Fig. 2) were significantly higher than the population mean based on 10 000 random permutations ($P < 0.01$). Four of the 11 clutches with parasitic offspring had mean r_{xy} values of host females and their parasitic offspring greater than or equal to what would be expected of half siblings ($r_{xy} = 0.25$). This level of relatedness could exist if the host female and the parasitic female were related at the level of full siblings or mother and offspring.

The frequency of clutches displaying EPF and IBP did not vary significantly between years (IBP $\beta_{\text{year}} = 0.0081$, $P = 1.0$; EPF $\beta_{\text{year}} = -1.04$, $P = 0.17$). In the high-density sites, five of 23 clutches (21.7%) showed evidence for EPF, compared with one of 19 clutches (5.3%) at the low-density sites. Likewise, five of 23 clutches (21.7%) at the high-density sites showed evidence of IBP, whereas six of 19 clutches (31.6%) showed evidence of IBP at the low-density sites (Table 1). Three clutches exhibited evidence of both EPF and IBP and all three were from high-density sites.

Based on the logistic regression model, the occurrence of IBP was not related to density or clutch size ($\beta_{\text{density}} = -0.57$, $P = 0.44$; $\beta_{\text{clutch}} = 0.28$, $P = 0.30$). Likewise, no effect of density or clutch size on the occurrence of EPF was found ($\beta_{\text{density}} = 1.30$, $P = 0.27$; $\beta_{\text{clutch}} = 0.19$, $P = 0.56$). Also, no effects of density or clutch size were found when both EPF and IBP were combined, i.e. the response variable (clutch) was coded as 1 if EPF and/or IBP was present and 0 if neither was present ($\beta_{\text{density}} = -0.45$, $P = 0.52$; $\beta_{\text{clutch}} = 0.31$, $P = 0.22$). The odds ratios for the effect of density on EPF and IBP were 5 (95% CI = 0.53–47.17) and 0.6 (95% CI = 0.15–2.40), respectively.

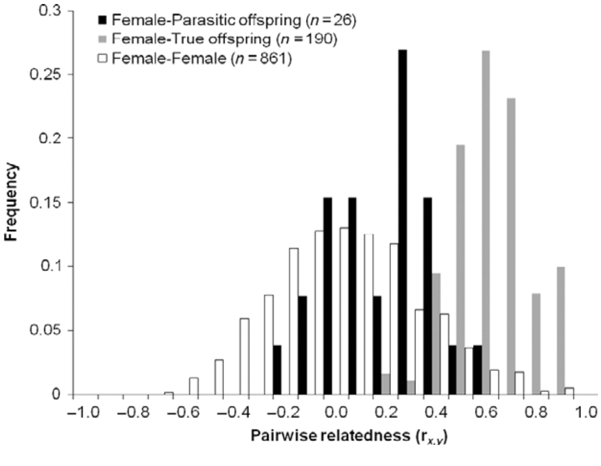

Figure 2. Frequencies of coefficients of relatedness between pairs of Canada Geese in southwest Michigan, including: (1) female–female comparisons, (2) females and their true offspring, and (3) host females and their parasitic offspring. Sample sizes reflect the number of pairwise comparisons included, and frequencies are based on those sample sizes.

DISCUSSION

This is the first study that we are aware of on parentage of a species of waterfowl nesting in an urbanized habitat. A positive relationship between nesting density and the frequency of alternative reproductive strategies was expected. However, we found no significant effect of density on the occurrence of IBP or EPF in clutches from natural (low-density) and urban (high-density) habitats, although the relationship between density and EPF was positive.

Among avian lineages, anatids exhibit some of the lowest rates of EPF. The reported frequency (percentage of clutches with at least one EPF chick) ranges from 0 to 13% (Triggs *et al.* 1991, Choudhury *et al.* 1993, Dunn *et al.* 1999, Griffith *et al.* 2002). Our frequency of 14% of clutches displaying EPF is close to this range, albeit at the upper end. However, intraspecific brood parasitism is common in waterfowl, with over 20 species exhibiting a frequency of at least 20% of nests parasitized (Rohwer & Freeman 1989, Zink 2000, Yom-Tov 2001). Therefore, our observed occurrence of clutches with IBP (26%) and EPF (14%) is comparable with the frequency of these alternative mating strategies in closely related waterfowl species that were studied under very different ecological conditions.

Investigation of the hypothetical relationship between density and the frequency of EPF has had mixed results. Studies that have corroborated this relationship were based mostly on observations of mating behaviour in colonial nesting species (Hamilton & Orians 1965, Birkhead 1978, Møller 1987, Lank *et al.* 1989, Møller & Birkhead 1993) under the assumptions that the rate of EPF is correlated with the observed rate of extra-pair copulations, and that colonial nesting species are typical of species with high nesting densities. As the number of empirical molecular studies investigating this relationship has increased, the emerging conclusion is that there is little evidence to support the relationship between breeding density and the rate of

EPF (Griffith *et al.* 2002). However, this may be due more to the lack of experimentally controlled studies than to the lack of a true biological relationship (Griffith *et al.* 2002).

Our results showed a trend toward higher rates of EPF at higher nesting densities. We observed a fourfold difference in rates of EPF (21.7% in high-density vs. 5.3% in low-density areas, Table 1), suggesting that results may be biologically meaningful, even though the relationship was not statistically significant. Small sample size (*n* = 42 clutches) and low rates of EPF in both densities may have hindered our ability to detect a statistically significant relationship. Thus, although it does not appear that high breeding density in areas of extensive habitat alteration has a significant impact on rates of EPF in urban Canada Geese, insufficient power may have limited our ability to conclusively determine this. Further study of the impact of anthropogenic habitat alteration on reproductive behaviour is needed to understand these relationships fully.

The frequency of IBP typically varies with factors that affect the availability of resources needed for breeding (de Valpine & Eadie 2008). For instance, breeding density is often invoked because increasing density decreases the availability of suitable nesting habitat (Haramis & Thompson 1985, Eadie 1991, Waldeck *et al.* 2004). We did not find a relationship between breeding density and the frequency of IBP in Canada Geese. This may be a reflection of the ability of Canada Geese to capitalize on a variety of different habitats available for nesting (Smith *et al.* 1999). Thus, nesting habitat may not be a limiting factor for Canada Geese in this system. Further experimental studies (e.g. Gowaty & Bridges 1991) would be necessary to confirm this speculation.

One factor that may have contributed to the evolution of IBP as an alternative reproductive tactic is the inclusive fitness benefits gained by host females if they have a familial relationship with nest parasites (Andersson 1984, 2001). For some broods, we found relatedness values of host and parasitic offspring that were indicative of sibling or mother–offspring relationships between the host and parasitic females. Female philopatry may lead to spatial clustering of related females over time (assuming these females all return to their natal breeding areas), thus increasing the likelihood of a parasitic female being related to her host by chance. In general, females may be more tolerant of the presence of related females, which could ultimately contribute to the unnaturally high goose densities that have developed at some sites where conspecific competition was once a limiting factor (e.g. Kaminski *et al.* 1979). Whether host females rear parasitic offspring of related females deliberately or by chance, and whether host females actually incur fitness benefits is unknown. Regardless of the mechanism or any underlying relationships, raising parasitic offspring is more costly to a host female's fitness than raising her own offspring. However, in urban environments, the abundance of food resources may mean that costs to rearing offspring, in terms of offspring survival and growth, are low (Balkcom 2010). Reduced selection pressures due to resource limitation could enable females to be more tolerant of brood parasitism in these environments because the female's own offspring have a higher probability of survival. Future studies addressing the effects of anthropogenic alteration of nesting habitat on levels of relatedness between host mothers and their parasitic offspring would be interesting.

Our study of Canada Geese indicates that the rates of EPF and IBP in this species do not vary significantly with respect to nesting density, and are therefore conserved across populations experiencing different population densities and habitats. Canada Geese are habitat generalists and are extremely adaptable to a variety of different social and ecological conditions (Mowbray *et al.* 2002). However, variation in population density and nesting habitat does not elicit a strong corresponding plasticity in reproductive behaviour. Observations of EPF and IBP in this urban/suburban population did not differ from rates of alternative reproductive strategies observed in closely related species in comparably pristine ecological conditions. Thus, proximate ecological conditions such as increased nest density, or relaxation of selection pressures (e.g. resource limitation) in urban settings, did not outweigh the evolutionary tendency for Canada Geese to employ a particular reproductive strategy.

Landscapes are being increasingly modified and species will continue to be affected by these modifications. Canada Geese represent a species that has shown a remarkable ability to adapt to human presence and to nest successfully in widely variable sites (Allan *et al.* 1995, Mowbray *et al.* 2002). Species whose reproductive behaviours are not strongly affected by varying ecological conditions, such as Canada Geese, may be better suited to adapt to the stresses imposed by increasing human population densities and associated urbanization. Conversely, species whose reproductive behaviours are highly plastic and are thus affected by ecological conditions that deviate from natural conditions under which they evolved (e.g. Wood Ducks, Semel *et al.* 1988) may be at greater risk of population declines due to social and demographic instability (Eadie & Fryxell 1992, Nee & May 1993).

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