2015

Parental Experience and its Effects on Reproductive Success in Common Loons

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Recommended Citation

Braden, Brandon S. MS, "Parental Experience and its Effects on Reproductive Success in Common Loons" (2015). *All Theses & Dissertations*. 174.
https://digitalcommons.usm.maine.edu/etd/174

PARENTAL EXPERIENCE AND ITS EFFECTS ON REPRODUCTIVE SUCCESS IN COMMON LOONS

A THESIS
SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF MASTER OF SCIENCE
UNIVERSITY OF SOUTHERN MAINE

BY
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2015

THE UNIVERSITY OF SOUTHERN MAINE
DEPARTMENT OF BIOLOGICAL SCIENCES

Date: 2-6-15

We hereby recommend that the thesis of **Brandon Braden**
entitled:

Parental Experience and its Effects on Reproductive Success in Common Loons

be accepted as partial fulfillment of the requirements for the degree of

Master of Science in Biology

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Acknowledgements

First off, I would like to thank Ann Perry who was always there with an answer when you needed information pertaining to anything that could possibly be needed last minute. I would like to thank my committee members, Dr. Terry Theodose and Dr. Jeff Walker, for helping me along the way with any questions that I had whether they pertained directly to this thesis or not. I would also like to thank the Biodiversity Research Institute for providing me with many years of data on breeding Common Loons and to all of their employees who helped to collect this invaluable field data over almost as many years as I have been alive. To my advisor, Dr. Jim Paruk, thank you for believing in me enough to invite me to study under you; I had all but gave up on going to graduate school and without your friendship and caring demeanor I do not think I would have gotten to the point that I am at today in my studies and life. Finally, an acknowledgement section is never long enough or thorough enough to truly recognize all the wonderful people that helped someone to get to the end point in their project. This thesis has been down a long road and there are many more people to thank than I possibly can acknowledge by name without inadvertently forgetting someone. To all my friends that have helped me along the way, whether through moral support or proofreading exercises, I thank all of you and owe you all more than you could possibly know.

Abstract

Common Loons (*Gavia immer*) are a highly territorial, long-lived species of waterbird that breed throughout the northern tier of North America. Loons form pair bonds seasonally, on their breeding territories, but overwinter separately. Much is known about environmental effects on loon reproductive success but little is known about how parental experience affects reproductive outcomes. I investigated the effects that individual experience and breeding pair length have on the reproductive success of Common Loons. The data I used were a compilation of individual territory occupancy and breeding records that were obtained by the Biodiversity Research Institute in Gorham, Maine from the years 1994-2011 on lakes that were studied in Maine, Massachusetts, New Hampshire, and New York. I predicted that as individuals and breeding pairs gained experience that their reproductive success would increase. I found no significant differences in reproductive success for any parameter, but I did find several trends. When looking at all individuals, there is a 5% increase in egg hatching success (p=0.12) with more experience; but, males with more experience increased egg hatching success by 8% (p=0.10) and females with more experience increased chick fledging success by 9% (p=0.09). However, males with more experience show no difference in chick fledging success and females with more experience show no difference in egg hatching success. I was not able to detect any trend in egg hatching or chick fledging success based on breeding pair experience. Future studies looking at the effect of age on reproductive success in Common Loons should be undertaken to further clarify if experience, age, or both may be playing a role in reproductive success.

Table of Contents

List of Tables

List of Figures

PARENTAL EXPERIENCE AND ITS EFFECTS ON REPRODUCTIVE SUCCESS IN COMMON LOONS

Brandon Braden

Introduction

In birds and mammals, individuals vary in reproductive success both within and between breeding seasons (Clutton-Brock 1988). An individual's age (e.g. Ainley and Schlatter 1972, Wooller and Coulson 1977), experience level (e.g. Nol and Smith 1987, Woodard and Murphy 1999), and environment (e.g. Holmes et al. 1996, Vieyra et al. 2009) have all been found to have direct influences on reproductive outcomes. Factors that affect one species are not always the same as those that affect others and they often interact to cause variability in success. Common Loons (*Gavia immer*) are a heavily studied species with copious amounts of unanalyzed data. As such, I chose to use a portion of a long-term set of data that were gathered by the Biodiversity Research Institute (BRI) in Gorham, Maine over a period of nearly 20 years to analyze their reproductive success.

Breeding makes considerable demands on adult birds (Wooller and Coulson 1977). Reproduction is a costly activity and has negative effects on the survival and future fertility of an individual (Partridge 1992). The most serious threat to adult survival is likely the energetic drain of provisioning offspring (Pugesek 1987, Pugesek 1990) as adults lose body mass throughout the course of the breeding season (Coulson et al. 1983, Monaghan et al. 1989, Pugesek and Diem 1990). The effort involved in each breeding attempt creates a balance between annual reproductive success and adult survival rates (Wooller and Coulson 1977).

Individual breeding success is age dependent in some birds (Newton 1992). Older individuals are usually more successful reproductively (Curio 1983, Clutton-Brock 1984, Sæther 1990) and the reproductive output of an individual increases with age (Ainley and Schlatter 1972, Wooller and Coulson 1977). Older birds are more attentive (Aldrich and Raveling 1983, Yerkes 1998) and fledge more young (Crawford 1977). Age significantly affected recruitment and brood success in Barnacle Geese (*Branta leucopsis*; Black and Owen 1995) and in Song Sparrows (*Melospiza melodia*) age was more important than breeding experience (Nol and Smith 1987). Even though breeding success has been shown to be age dependent in birds, in some species breeding experience, irrespective of age, is more important (Newton 1992).

When looking at reproductive success, taking into account only one member of a breeding pair represents only half the picture (Black and Owen 1995). Reproductive success is known to be higher in pairs with experienced breeders (Wooller and Coulson 1977, Nol and Smith 1987, Reid 1988a, Sæther 1990, Smith 1993, Woodard and Murphy 1999, Angelier et al. 2007). However, variation exists in how experience within a breeding pair influences success. Little Penguins (*Eudyptula minor*) experience higher success rates in pairs that have been together longer (Nisbet and Dann 2009). In Eastern Kingbirds (*Tyrannus tyrannus*), pairs where both individuals were experienced lost the fewest individuals due to starvation but fledging success did not differ as long as one individual in the breeding pair was experienced (Woodard and Murphy 1999).

Multiple hypotheses exist to predict why an individual or breeding pair will experience an increase in reproductive success with age and experience. The breeding experience (Nol and Smith 1987), parental experience (Lack 1966, Nur 1984, Nol and Smith 1987), and reproductive effort (Williams 1966, Gadgil and Bossert 1970, Pianka and Parker 1975, Charlesworth and Leon 1976) hypotheses are prominent examples in the bird literature. Any of these hypotheses, as well as others, may be able to explain variations in breeding success.

Breeding places greater demands on first-time breeders (Wooller and Coulson 1977). The breeding experience hypothesis states that previous breeding experience improves breeding performance (Nol and Smith 1987). First-time breeders generally occupy lower quality territories (Pugesek and Diem 1983, Reid 1988b, Pärt 2001) and produce fewer young (Lack 1968, Perrins and Moss 1974). In contrast to first-time breeders, reproductive success is higher in pairs with experienced breeders (Wooller and Coulson 1977, Nol and Smith 1987, Reid 1988a, Sæther 1990, Smith 1993, Woodard and Murphy 1999, Angelier et al. 2007). Improved success with experience has been attributed to familiarity between individuals within the breeding pair (Scott 1988, Reid 1988a, Black and Owen 1995), improved feeding efficiency (Lack 1966, Orians 1969, Crawford 1977, Limmer and Becker 2009), and increased predator avoidance (Crawford 1977). Individuals with prior breeding experience also tend to return to breeding sites and initiate a nest earlier, which has been shown to increase success (Ainley 1975, Wooller and Coulson 1977, Nol and Smith 1987, Woodard and Murphy 1999).

The parental experience and reproductive effort hypotheses are two similar theories that try to further explain why an individual or breeding pair becomes more successful with age and experience. Older adults are known to spend more time foraging (Pugesek 1981) and foraging efficiency increases with age (Pugesek 1983). The parental experience hypothesis specifically assumes that an older adult can gather food more efficiently, which allows them to provide more food to their offspring (Lack 1966, Nur 1984). The reproductive effort hypothesis assumes that older adults provide more food to their offspring by working harder at foraging (Williams 1966, Gadgil and Bossert 1970, Pianka and Parker 1975, Charlesworth and Leon 1976). Studies on foraging behavior in California Gulls (*Larus californicus*) have been the primary source for research on these two hypotheses and the results support the reproductive effort hypothesis (Pugesek 1981, Pugesek 1983, Pugesek 1995).

Many studies have measured reproductive success in long-lived species of birds (Newton 1992). Two marked population studies reveal that only some individuals that survive to reproductive age breed successfully and the most successful individuals in a population contribute disproportionately to the next generation (Newton 1992, Torres et al. 2011). Breeding success has been shown to improve annually during the early years (Sæther 1990, Martin 1995, Ezard et al. 2007) and many species have also been shown to have a gradual decline later in life (Ollason and Dunnet 1988, Scott 1988, Wooller et al. 1989, Pugesek and Diem 1990, Black and Owen 1995, Nisbet and Dann 2009, Torres et al. 2011, Mauck et al. 2012). Age related wear and tear of breeding and competing has been implicated in this age related decline in success (Clutton-Brock 1984, Newton 1992). Also, older parents may provide less or poorer parental care (Beamonte-Barrientos et al. 2010).

Gaviiformes is a monophyletic order (Genus *Gavia*) that consists of five long-lived and highly territorial species of waterbird (Lindsey 2002). Most previous studies on reproductive success in long-lived birds have been on waterbirds in the order *Procellariiformes* (e.g. Mauck et al. 2004, Mauck et al. 2012), *Charadriiformes* (e.g. Pugesek 1981, Pugesek 1983, Pugesek and Diem 1983), or *Sphenisciformes* (e.g. Ainley and Schlatter 1972; Hackett et al. 2008). However, these orders consist of species that are colonial to semi-colonial in their nesting habits, which is very different from the territorial nature of species in the order *Gaviiformes*.

Common Loons (*Gavia immer*) are highly territorial and nest solitarily. It is unknown if the same reproductive principles that apply to colonial and semi-colonial nesters also apply to loons. Since the 1970's, Common Loons have been studied in depth in the United States. In the late 1980's, a new capture technique (Evers 1993, Evers 2001) allowed for banding and color-marking of loon individuals allowing for more robust studies and the tracking of individuals over a lifetime. The objective of this study was to use a large, long-term dataset on marked Common Loons in the northeastern United States to assess whether experience plays a role in reproductive success. I hypothesized that as individual loons gained experience that their reproductive success would increase. I further hypothesized that breeding pairs with more experience would also show an increase in reproductive success.

Common Loons as a Study Species

The Common Loon is a large (2700-7600 kg) waterbird that is considered to have a fairly stable population throughout its range (Evers et al. 2010, Gray et al. 2014). Their breeding range encompasses northern portions of the contiguous United States, most of Canada and Alaska outside of the High Arctic, Greenland, and Iceland (McIntyre 1988; Figure 1). Loons breed on large freshwater lakes that generally have clear water, irregular shorelines, an abundance of fish, and numerous small islands (Evers et al. 2010). Because their habitat requirements have been impacted in parts of their range, the species has received much attention from conservation biologists.

Figure 1. Common Loon breeding and wintering range in North America (Evers et al. 2010).

Numerous factors have been found to affect Common Loon breeding success. Loons have been shown to be negatively affected by human disturbance, but most studies have shown little to no effect on breeding success attributed to human caused disturbance (McIntyre 1975, McIntyre 1988, Titus and VanDruff 1981, Caron and Robinson 1994, Badzinski and Timmermans 2006). Lakes with more cottages have a lower probability of loon nest success, but once hatched, chick fledging is independent of human recreational activities (Heimberger et al. 1983, DeSorbo et al. 2006). One study even showed an increase in the number of chicks fledged on lakes with more intensive development (McIntyre 1988). Human development can also affect loons by increasing the presence of nest predators (McIntyre 1988) with raccoons (*Procyon lotor*) considered the most significant loon egg-predator (Sutcliffe 1980, McCann et al. 2004, Meyer 2006).

Many lake characteristics have also been shown to affect Common Loon reproductive success. Loons are more productive on larger, clearer, and more alkaline lakes (Alvo et al. 1988, Alvo 2009), but they still breed successfully on lakes with limited water clarity (McIntyre 1975). On turbid bodies of water, only shallow, marshy back bays and inlets are adequate as habitat (Barr 1986). Man-made reservoirs can negatively affect loon nesting success through nest flooding or water drawdowns (Fair 1979, Reiser 1988, Windels et al. 2013), but reservoirs can also create new habitat (McIntyre 1994). Lakes with elevated methylmercury levels have been shown to have significant negative effects on loon reproductive success (Evers et al. 2008, Burgess and Meyer 2008). Waterbodies with fluctuating water levels, such as reservoirs, can increase the methylation of inorganic mercury (Kelly et al. 1997). Finally, the probability of a loon pair raising two chicks is correlated with higher dissolved organic carbon levels but no relationship was found when only one chick was raised successfully (Badzinski and Timmermans 2006).

Common Loons are both seasonally and genetically monogamous, but breeding pairs do not persist outside of the breeding season (Piper et al. 1997a). Pairs remain together, on average, five years with 11 years being the longest confirmed (Evers 2001). Overall, the pair turnover rate in loons is approximately 20-23% per year – 7% by passive occupation when a mate fails to return and 8-

9% by active occupation from intrasexual competition (Piper et al. 2000, Evers 2001, Paruk 2006, Evers et al. 2010). When a pair member does not return, a new mate is usually found quickly (Evers et al. 2010).

Loons are highly territorial during the breeding season. Males typically arrive to the breeding grounds first, shortly after ice out, with previous territories being occupied before transitional territories (Evers et al. 2010). Competition over breeding territories is created by the intrusion of non-breeding loons on established breeding territories (Piper et al. 1997b, Paruk 2006, Piper et al. 2006). Territorial takeovers usually occur before nesting is initiated or shortly after a failed nesting attempt (Evers et al. 2010). Individuals have been known to remain on the same territory for up to 17 years but may take 1-3 years to establish a new breeding territory if replaced by another individual (Evers et al. 2010).

Common Loon Breeding Biology

On average, Common Loons delay breeding for six years after fledging (Evers et al. 2000). Most loon nests are constructed in May or June, but the egg-laying date is generally dependent on latitude (Evers et al. 2010). Nests may be built directly on the ground, on a floating sedge mat, or more recently on artificially constructed platforms (DeSorbo et al. 2006). Loons prefer island sites over mainland sites for nesting and both adults contribute equally to construction (McIntyre 1975, McIntyre 1988). Nests are generally built adjacent to deep (1m) water with a steep incline (Evers et al. 2010). Incubating loons have few predators, but Bald Eagles (*Haliaeetus leucocephalus*) have been known to attack them (Vlietstra and Paruk 1997).

Egg-laying begins just before or shortly after the nest site is completed (Evers et al. 2010). Only one brood is raised per year, but loons may attempt to re-nest depending on when the nest is lost (Evers et al. 2010). Replacement clutches are laid 8-19 days after nest loss with longer intervals occurring later in the season (Yonge 1981). Incubation lasts approximately four weeks and both parents share incubation responsibilities (Paruk 1999).

Offspring are semiprecocial and rely on their parents for brooding, food, and protection for several weeks after hatching (Evers et al. 2010). Chicks are entirely dependent on their parents for food at first, but they capture about 50% of their food by week 8 and 90-100% by week 11 (Evers et al. 2010). Chicks begin to exercise their wings around week 8 (Barr 1973, Barr 1996), but their first take-off may be delayed until week 12 or 13 depending on weather (Evers et al. 2010). Juveniles become independent as they begin to fly and catch their own food, but typically at least one parent stays with the offspring until they are at least 12 weeks old (Evers et al. 2010). Juveniles usually remain on their natal lake for an additional 1-3 weeks after the parents leave (Evers et al. 2010).

Methods

Study Area and Data Collection

From 1994-2011, the Biodiversity Research Institute in Gorham, Maine and their partners have been conducting research and gathering data on

Common Loon reproductive success in Maine, Massachusetts, New Hampshire, and New York (Figure 2). They have done this primarily through marking and monitoring individuals through time. During the summer, individual loons were captured at night using a combination of boats, spotlights, loon vocal recordings, and fish landing nets (Evers 1993, Evers 2001). Captured individuals were fitted with a metal United States Fish and Wildlife Service identification band and plastic color bands in unique combinations and then released. The unique combination of bands allowed for identification without recapture in subsequent years. On a yearly basis, data were collected on marked individuals that occupied monitored territories.

Breeding surveys were conducted every five to seven days from May through July during the peak loon nesting and hatching periods. On surveys, previously occupied loon territories were visited and pairs were located to determine if a loon pair was nesting and if eggs had hatched. All known nests sights were checked regularly for signs of nesting. Trained observers used 10x binoculars or 15-45x spotting scopes from boat or shore to observe loons and their behavior. Color bands were observed opportunistically during surveys and bands sighted in the field were recorded for later identification of the individual(s). When chicks were successfully hatched, breeding surveys were continued weekly from August to September to determine chick survival. Any chick that survives past six weeks is considered to have fledged as chicks rarely die beyond this age (Evers et al. 2010).

Figure 2. Location of study area and lakes where Common Loon nests were monitored during the 1994-2011 breeding season.

Statistical Parameters

The number of eggs hatched and chicks fledged on each territory was used to establish the percentage of eggs hatched (PEH) and percentage of chicks fledged (PCF) in a specific year. The PEH was calculated by dividing the number of eggs hatched by two because a loon nest rarely deviates from two eggs (Evers et al. 2010), there were no data on the number of eggs a nest had, and there was no way to tell if only a single egg was laid or if the second egg was predated or lost prior to observer arrival. The PCF was calculated by dividing the number of chicks fledged by the number of eggs hatched.

Individual and Breeding Pair Success

To assess individual and breeding pair success, the PEH and PCF for a territory in a given year were assigned to any adult individual that was recorded on the territory. If the male and female members of a breeding pair were known, then a territory's PEH and PCF values in a given year were assigned to the pair. If an individual or breeding pair did not have at least two years of data, they were excluded from the analysis.

To assess whether a change in success was occurring with increased experience, the mean PEH and PCF values were calculated for the first and second half of each individual's and breeding pair's experiences. A difference in the mean PEH and PCF values was then calculated for each individual and breeding pair. To calculate the difference in means, the mean PEH or PCF value from the first half of an individual's or breeding pair's observations were subtracted from the mean PEH or PCF value from the second half of the observations respectively. In the event that an odd number of observations occurred, the middle value was excluded from the analysis. A positive difference between PEH or PCF values indicated an increase in success with more experience and a negative difference indicated a decrease in success. Finally, a grand mean was then calculated from all the difference in mean calculations.

Because I predicted an increase in success with experience, a one-tailed test was used with an alpha of 0.05. To calculate p-values, the PEH and PCF values for each individual or breeding pair were randomly permuted and the difference in means were recomputed in order to obtain a new grand mean. This process was completed a total of 999 times for a total sample size of 1000 grand means per analysis; the number of times that a randomly permuted grand mean was greater than or equal to the measured grand mean were totaled and divided by 1000 to obtain a p-value. R (version 2.15.3) was used for all statistical analyses (R 2013).

Environmental Variables

Most environmental effects were excluded from the analyses as they were uncontrollable. Although environmental factors have been found to be important in nesting success (e.g. McIntyre 1975, Barr 1986, Alvo et al. 1988), all individuals and pairs were on the same lake for the entirety of their recorded experience. Therefore, environmental factors were deemed to be a constant variable in the analyses and if experience was playing a role in success, then a change in success should have been apparent. However, because nest site type could vary from year to year and data were available, these factors were analyzed for potential effects using a one-way ANOVA to determine if the different nest site types could be analyzed concurrently or if they needed to be analyzed separately.

Results

No difference in success was found in PEH (p-value = 0.67) or PCF (p-value = 0.45) based on nest site type (Figure 3). Therefore, analyses were based on all individuals and pairs for the remainder of the study, regardless of nest site type.

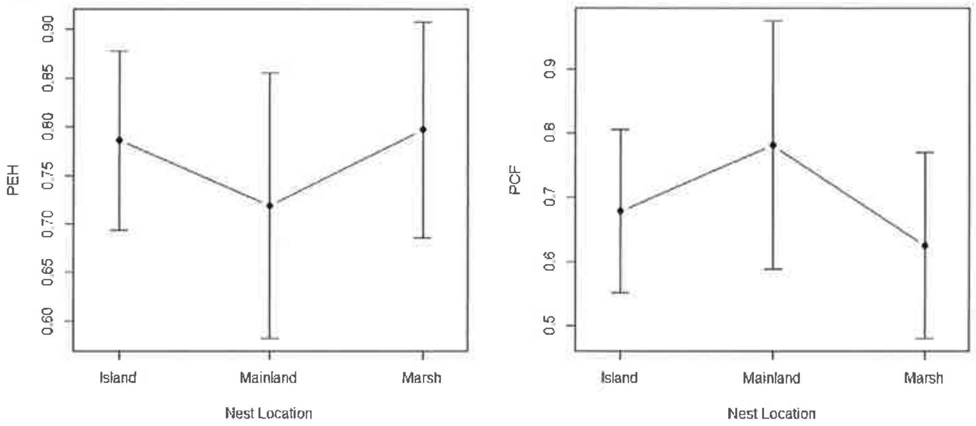

Figure 3. Analyses showing no difference in Common Loon PEH (p-value = 0.67) or PCF (p-value = 0.45) success based on nest site type.

I analyzed measures of Common Loon breeding success on 91 individuals, each with 2 to 6 independent observations. The PEH showed a 5% increase (p=0.12) and the PCF showed a 3% increase (p=0.26) but overall no significant differences were found between individual experience and loon reproductive success (Table 1). I analyzed breeding pair success on 19 pairs, each with 2 to 5 independent observations. The PEH showed a 1% decrease (p=0.47) and the PCF showed a 1% increase (p=0.48) but overall there was no significant difference in PEH or PCF based on breeding pair experience (Table 1).

Table 1. The percent change in Common Loon eggs hatched and chicks fledged for all individuals and breeding pairs with increased breeding experience.

	Success Measure	**Percent Change**	**P-Value**
Individuals	PEH	+5%	0.12
	PCF	+3%	0.26
Breeding pairs	PEH	-1%	0.47
	PCF	+1%	0.48

I further analyzed individuals by sex. Male analyses were conducted on 47 individuals, each with 2 to 6 independent observations; female analyses were conducted on 44 individuals, each with 2 to 5 independent observations. Males showed an 8% increase in PEH (p=0.10) and a 3% decrease in PCF (p=0.34). Females showed a 1% increase in PEH (p=0.46) and 9% increase in PCF (p=0.09). Again, no significant differences were found for any analyses, but the increase in male PEH and female PCF both approached significance (α = 0.5; Table 2).

Table 2. The percent change in Common Loon eggs hatched and chicks fledged for male and female individuals with increased breeding experience

Sex	Success Measure	Percent Change	P-Value
Male	PEH	+8%	0.10
	PCF	-3%	0.34
Female	PEH	+1%	0.46
	PCF	+9%	0.09

Discussion

Many avian studies have shown that individuals and breeding pairs with experience are more successful at hatching and fledging young (Wooller and Coulson 1972, Nol and Smith 1987, Reid 1988a, Sæther 1990, Smith 1993, Woodard and Murphy 1999, Angelier et al. 2007). However, this study found no evidence to support the hypotheses that as individual loons and breeding pairs gained experience they would increase their reproductive success. At best, increased individual experience may influences egg hatching and chick fledging success in a sex specific fashion; however, further research is needed to definitively answer these questions.

One factor that has been shown to have major impacts in loon reproductive success is mercury levels (Evers et al. 2008, Burgess and Meyer 2008). Mercury data was available from BRI for many of the individuals in this study, but I was unable to further analyze its effects because the data breaks the assumptions of normality and equal variances. These assumptions are necessary to meet in order to get an accurate portrayal of the data.

Of the three hypotheses that were discussed in the introduction (breeding experience, parental experience, and parental effort), the only one that is currently testable in loons is the breeding experience hypothesis. This is because the breeding experience hypothesis simply states that previous breeding experience improves breeding performance (Nol and Smith 1987). This hypothesis can be tested regardless of age and other factors.

The parental experience and parental effort hypotheses are not testable in this study. In order to test these hypotheses, observations would need to be made in the field on the foraging efficiency and parental effort of known age individuals. Currently, there are methods that allow for individual aging in birds (Fallon et al. 2006, Cooey 2008), but these methods have been unsuccessful with Common Loons (J. Paruk, unpublished data) making chick banding a priority if age measurements are to be used. Similarly, in order to assess parental effort, measurements of effort had to be taken during the years that the data on territory success were obtained.

Male Effects

Male Common Loons with more experience showed an 8% increase in hatching success ($p=0.10$) but a 3% decrease in fledging success ($p=0.34$; Table 2); however, neither result was significant. Despite the lack of significance, the 8% increase in hatching success approached significance ($\alpha = 0.5$; p-value = 0.10) and a study by Piper et al. (2008) did show a similar increase in success for male loons. In Wisconsin, it was found that when a male remained on a territory for multiple years that they increased their nesting success by 41%; however, success was narrowly defined by whether the nest hatched or was predated (Piper et al. 2008).

Interestingly, male loons are responsible for nest site selection (Piper et al. 2008). Many species of bird follow the 'win-stay, lose-switch' rule (e.g. Newton 1976, Styrsky 2005). Simply stated, the 'win-stay, lose-switch' rule suggests that if a nest-site is successful then it makes sense to stay but if it fails then a new site should be used (Haas 1998, Hoover 2003). Any egg that fails to hatch is considered an energetic loss for the individual that laid the egg and any individual that incubated it (Koenig 1982). The primary reason that loon nests fail is due to predation, with raccoons alone causing 37-79% of nest failures; if a predated nest is reused, the same outcome typically occurs (Sutcliffe 1980, McCann et al. 2004). Piper et al. (2008) suggested that male loons follow the 'win-stay, lose-switch' rule because as long as the same male remains on a territory a successful nest-site is generally reused. By reusing previously successful nest sites, male loons are insuring that their nest will have a good chance of succeeding again whereas avoiding nest sites that were depredated or otherwise lost is an overall good strategy to reduce the likelihood of losing another nest.

An increase in egg hatching success may also indicate that males become more attentive to their nests as they gain experience. Loons share incubation responsibility (McIntyre 1988, Paruk 1999) and in species where both parents incubate, the coordination of activities between partners is important for preventing egg predation and chilling (Bukacińska et al. 1996). Nest attentiveness in loons has been found to influence nesting success because nests with a lower percentage of incubation coverage (<91%) are typically less successful (Paruk 1999, Cummings 2003). An individual's inability to meet increased incubation demands can also have a negative impact on embryo development and survival (Thomson et al. 1998, Engstrand and Bryant 2002). Why a male loon would become more attentive to its nest with experience is unknown; unfortunately, the link between experience and reproductive success is often unclear (Hipfner et al. 2002). However, a change in hormone levels may be responsible (Pugesek 1995, Angelier et al. 2007, Riechert et al. 2012).

Prolactin and corticosterone are two hormones that are involved in breeding; high prolactin is needed to express breeding behavior and corticosterone is related to activity or stress (Riechert et al. 2012). Hormone levels in birds vary with age and individuals with low prolactin and elevated corticosterone levels are the least likely to successfully fledge young (Angelier et al. 2007, Riechert et al. 2012). In Black-browed Albatross (*Thallasarche melanophris*), prolactin levels slowly increased with experience but only corticosterone levels were found to affect chick fledging success (Angelier et al. 2007). Low hormone levels during the first years of breeding could indicate that the endocrine system is unable to secret the necessary hormones or it might indicate a down-regulation to limit parental expenditure (Riechert et al. 2012). At this point, little is known about hormone levels in loons. However, assuming prolactin levels increase in loons as they get older, this may affect nest site attentiveness and egg hatching success in males.

Female Effects

Female Common Loons with more experience showed a 1% increase in hatching success (p=0.46) and a 9% increase in fledging success (p=0.09; Table 2); neither result is significant but the 9% increase in fledging success approaches significances (α = 0.5; p-value = 0.09). There are multiple explanations as to why female loons may be influencing fledging success including egg quality and provisioning skills.

Older females may produce eggs that are larger and of higher quality as egg-size can very as much as 30% in loons within the same region (Evers et al. 2010). Egg size was critical in determining reproductive success in Thin-billed Prions (*Pachyptila belcheri*) and the effects of egg size lasted through fledging (Silva et al. 2007). Egg components such as lipids, proteins, and water increase with age in female birds (Bogdanova et al. 2006). Higher quantities of important egg components may result in more fit offspring with a better chance of survival to fledging.

More experienced females may also be better at providing for their offspring once hatched. In loons, both parents stay with the chicks and feed them for the first few weeks after hatching; but comparatively, males spend more time performing vigilant behaviors while the female does more of the foraging (Mager 1995, Paruk 1999). Experienced Northern Goshawk (*Accipiter gentilis*) mothers fed their young more frequently regardless of prey density (Byholm et al. 2011) and experienced Common Terns (*Sterna hirundo*) delivered prey items of higher energy content (Limmer and Becker 2009). More frequent feeding and higher energy food items directly affect chick growth rates and possibly survival (Pugesek 1995). If experienced female loons feed their young more or higher quality food items, this may influence chick fledging success.

As in males, hormones may be affecting the ability of a female loon to successfully fledge offspring. In Black-browed Albatross only corticosterone levels were found to affect chick fledging success with the most successful individuals having lower levels or corticosterone; lower corticosterone levels are associated with less stress and decreased activity (Angelier et al. 2007; Riechert et al. 2012). Corticosterone may also play a role in chick fledging success in loons. Females with more experience on their territory may be more efficient at catching prey and spend less time foraging; less time spent foraging could decrease corticosterone levels through a decrease in activity.

Breeding Pair Effects

Breeding pairs with more experience showed a 1% decrease in percentage eggs hatched (p=0.47) or and a 1% increase in percentage chicks fledged (p=0.48) in this study (Table 1); however, neither result approached significant levels. Even though experienced breeding pairs show no difference in egg hatching or chick fledging success, there may be other ways that these pairs influence their overall reproductive success. Juvenile loons suffer an estimated 25% annual mortality rate in their first three years of life (59% overall), much higher than the adult rate of 8% per year (Mitro et al. 2008, Evers et al. 2010). Juveniles raised by more experienced breeding pairs may be of higher quality and less likely to suffer mortality during the first three years of life. Experienced Blue-footed Boobies (*Sula nebouxii*) produced higher quality offspring with a greater probability of recruiting into the breeding population (Torres et al. 2011) and parental experience in Thick-billed Murre (*Uria lomvia*) was found to influence chick growth rates (Hipfner et al. 2002). If experienced loon pairs produce higher quality chicks with a better chance of survival, their offspring would contribute disproportionately to the next generation.

Pair turnover may be an indicator of whether breeding pairs that remain together longer have a higher success rate, whether through measurable reproductive output or higher quality offspring. Turnover in birds should not occur unless it leads to an increase in reproductive success (Choudhury 1995). Common Loons experience an annual pair turnover rate of only 7% when only taking into account when a mate fails to return (Piper et al. 2000, Evers 2001, Evers et al. 2010). The low pair turnover rate from passive occupation in loons suggests that breeding pair length may affect reproductive success, possibly through higher quality offspring.

Previous analyses have found that Common Loon breeding pairs with more experience do have an effect on reproductive success. In Vermont, it was found that established pairs had a higher nesting success rate, higher chick productivity rate, and were more likely to make a nesting attempt (Hanson and Buck 2009). However, the results in Vermont were never published and nesting success was broadly defined as whether any egg(s) hatched. Also, nesting success and chick fledging rates included pairs that did not attempt to breed in a given year whereas this study only looked at success in years where individuals were known to have made a breeding attempt. Of note, in Vermont it was also found that established pairs were more likely to use islands and artificial nesting rafts, which have been shown to increase loon nesting success (DeSorbo et al. 2006, Hanson and Buck 2009).

Compared to colonial and semi-colonial nesting birds, we know relatively little about Common Loon nesting success. Many of these colonial and semi-colonial species peak in breeding success around the time that they reach their average life expectancy (e.g. Scott 1988, Wooller et al. 1989, Black and Owen 1995) while others peak around mid-life (e.g. Ollason and Dunnet 1988). The annual survival rate for adult Common Loons is estimated at 92% (Mitro et al. 2008). Because this number represents an average survival rate for unknown age adults, it provides the average for a cohort of breeding adults that were followed for 1-14 years (Evers 2001). On average, loons delay breeding for six years so this would assume a life expectancy of around 20 years (Evers et al. 2000, Evers 2001). Loons are known to surpass this age, but it is unknown whether this is the exception or the rule. Without having the ability to test these data with known ages of loons, it is impossible to tell if loons peak in success around their average life expectancy, in mid-life, or perhaps they may never peak; this could be a significant confounding factor in this study that cannot be accounted for at this time. It is well documented that loon nesting success is affected by environmental conditions (e.g. Fair 1979, Kelly et al. 1997, Badzinski and Timmermans 2006, Evers et al. 2008) and perhaps this is ultimately the primary driving factor in their reproductive success.

Some avian species also show a distinct increase in reproductive success during the first few years of breeding followed by a relatively stable period. The egg hatching success in Leach's Storm-Petrel (*Oceanodroma leucorhoa*) has been shown to improve dramatically during the first 2-4 years of breeding but then remains relatively constant up until the last two years before death (Mauck et al. 2004, Mauck et al. 2012). Even though only small increases in reproductive success were found in loons, they may experience more dramatic changes early in their reproductive lifetime similar to Leach's Storm-Petrel. Again, the only way to determine this would be to obtain a sample of known age individuals and follow them closely from their initial breeding attempts until they are no longer a part of the breeding population.

Conclusions and Recommendations

This study was able to look for general trends in Common Loon reproductive success rates. However, I was unable to determine if there are distinct periods of time where loons increase (or decrease) in success, if their success increases continually over their lifetime, or if their success is relatively constant and affected more by their environment. I was also unable to determine whether experienced breeding pairs produced higher quality offspring that were more likely to survive until breeding age or if hormone levels may be playing a role in reproductive success.

The only way to currently obtain known age individuals in loons is to band chicks. However, even if an individual is banded as a chick, it is unlikely that the bird will be seen again. Of the nearly 600 juveniles that were been banded in 17 years of research, only 2 have actually been recorded as returning to a lake that was studied and had associated nesting records. Possible ways to overcome this would be to band more juveniles and expand resighting efforts, utilize a form of satellite or radio telemetry to follow known age individuals as technology becomes better and more affordable in this area, or develop a way to age adult individuals from blood or other biological samples that can be obtained in the field. Along the same lines, the only way to identify if higher quality individuals are being raised by more experienced parents would be to develop a technology that allows for the juveniles to be accurately followed for several years, at least until they reach breeding age, to more accurately assess juvenile survival rates.

The BRI has blood samples archived from many of the individuals they have captured from 1990 to the present. It may be possible that someone could test blood samples from individuals that were followed until chick loss or chick fledging to determine if hormone levels play a role in the ability of Common Loons to successful raise their offspring. Unfortunately, loons are currently only captured once their eggs have hatched and the chicks are a few weeks old, which means blood samples from individuals that failed to hatch eggs is almost non-existent. The only way to fully know if hormones affect egg hatching or chick fledging success would be to employ an infrequently used method of capture for Common Loons, which requires capturing the loons on their nest during incubation and then correlating egg hatching and chick fledging success to blood hormone levels. Due to the intrusive nature of this capture technique, an alternative would be to use blood samples collected from a closely related superspecies, the Yellow-billed Loon (*Gavia adamsii*), which is already captured with the on-nest method. Blood samples from Yellow-billed loons could be tested and correlated to their egg hatching and chick fledging success and if a difference exists then it may be advantageous to conduct a similar study on Common Loons.

Lastly, I would recommend that a concerted effort be made to increase band resighting efforts, especially of adults banded as juveniles. Of the 4060 territory records, I was able to correlate an individual to a territory that had at least two years of information 248 times, which led to a total of only 91 individuals with at least two years of data. Of those 248 territory records with known individuals only 12 failed to hatch at least one chick for a 5% nest failure rate, and no territory had recorded individuals that didn't attempt at least one nest. However, of the 4060 territory records with at least one territorial pair, only 2626 had at least one nest attempt and 1132 failed to hatch a nest at all for a total of 43% of the territories that attempted a nest failing before the eggs hatched; a percentage much higher than for territories that had a nesting attempt and at least one known individual. This means that when a nest fails or a nesting attempt is never made, we rarely know what individual was on that territory. Having most of my data involving at least a successful nesting attempt is not consistent with the general nesting success data, which means my data are not representative of the general reproductive picture. Some of the reason for this is that if no eggs hatch and especially if no nesting attempt is made, then it is all but impossible to capture the adults and band them if they have not been previously banded. Moreover, I suspect that once a nest fails, individual resighting efforts are reduced, leaving already banded individuals with failed or never attempted nests largely unrepresented in the data for the year.

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