Management and Conservation Note

Breeding Propensity of Female Harlequin Ducks

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ABSTRACT Breeding propensity, the proportion of sexually mature females that initiate egg production, can be an important demographic trait when considering reproductive performance and, subsequently, population dynamics in birds. We measured egg production using yolk precursor (vitellogenin and very-low-density lipoprotein) analyses and we measured nesting using radiotelemetry to quantify breeding propensity of adult female harlequin ducks (*Histrionicus histrionicus*) in British Columbia, Canada, in 2003 and 2004. Using both methods combined, and accounting for error rates of each, we estimated that breeding propensity of adult females that migrated to breeding streams was 92%. These data suggest that, despite speculation that harlequin ducks have low breeding propensity, almost all adult females on our study site were not constrained in their ability to produce eggs and that influences on reproductive performance at later stages likely have much stronger effects on population dynamics. (JOURNAL OF WILDLIFE MANAGEMENT 72(6):1388–1393; 2008)

Overall reproductive performance is the product of success across a series of reproductive stages including breeding propensity, which we define as the proportion of females that initiate egg formation (the inverse of nonbreeding). The literature is replete with studies describing rates of avian reproductive performance at most stages, such as nesting success and brood survival; however, breeding propensity has been poorly documented. Estimates of nonbreeding rates suggest that this behavior can be extensive in some species, especially seabirds (Coulson 1984, Cam et al. 1998). Nonbreeding by sexually mature individuals often is viewed in the context of life-history theory as a trade-off between current and future reproductive potential (Stearns 1992, Chastel et al. 1995, Golet et al. 1998). Thus, nonbreeding has been proposed as an adaptive strategy for long-lived species under certain conditions (Wooller et al. 1990). Proximate factors suggested to influence rates of nonbreeding include body condition and inter-individual variation in quality (Drent and Daan 1980, Coulson 1984, Mills 1989, Johnson et al. 1992, Cam et al. 1998). Rates of nonbreeding are likely affected by multiple causes and individual state, as well as external factors such as food availability or severe environmental variability, are both influential (Cam et al. 1998). Documentation of breeding propensity is important from a management perspective, because it allows consideration of the stages and mechanisms by which reproductive effort may be constrained (Cam et al. 1998). For example, low rates of breeding propensity may indicate poor habitat conditions, such as poor food availability or low nest-site availability, whereas poor nesting or brood success may be the result of high predation rates or inclement weather. Differentiating between these stages and causes of poor reproductive performance allows management to be targeted at the appropriate reproductive stage for maximum effect.

Sea ducks generally (Coulson 1984, Goudie et al. 1994, Quakenbush and Suydam 1999), and harlequin ducks (*Histrionicus histrionicus*) specifically (Bengtson and Ulfstrand 1971, Robertson and Goudie 1999), have been speculated to show a high degree of nonbreeding, which could have important implications for population-level productivity. Harlequin ducks are of management concern, in part because productivity has been suggested to be too low to compensate for observed mortality rates (Smith et al. 2001). Productivity has been quantified on specific breeding streams (see Robertson and Goudie 1999), as well as more regionally via measurement of age ratios on wintering areas (Smith et al. 2001, Rodway et al. 2003). Other demographic characteristics that have been described for harlequin ducks include measures of survival, both annually (Cooke et al. 2000) and seasonally, including during winter (Esler et al. 2000), wing molt (Iverson and Esler 2007), and the breeding season (J. C. Bond, Simon Fraser University, unpublished data). Also, the demographic consequences of dispersal have been considered (Cooke et al. 2000, Iverson et al. 2004, Iverson and Esler 2006). A clear understanding of the causes of low productivity in harlequin ducks still is lacking and, therefore, further quantification of demographic attributes, including reproductive performance metrics such as breeding propensity, is warranted to identify when and where constraints on population dynamics are expressed.

Reported rates of breeding propensity by harlequin ducks are highly variable (18–92%), as are the methods employed to obtain them (Table 1). One of the primary concerns with most methods used to date is that they cannot distinguish between true nonbreeders (i.e., those F that do not initiate clutch formation), and females that fail early in the egg production or incubation stages. Thus, estimates of

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Table 1. Published harlequin duck breeding-propensity estimates and methods.

Region	Yr of study	Breeding propensity (%)	Method	Reference
Iceland	1965–1969	70–85	Proportion of F in flocks during Jun and Jul	Bengtson and Ulfstrand 1971
Iceland	1970	18	Proportion of F in flocks during Jun and Jul	Bengtson and Ulfstrand 1971
AK	1979–1980	50–53	Brood patch and behavioral observations	Dzinbal 1982
AK	1991–1992	74–86	Examination of cloaca and brood patch; presence of egg in abdomen	Crowley 1999
WY	1985–1986	38	Mass of captured F	Wallen 1987
OR	1995–1996	49	Repeat observations of F in single or mixed-sex groups	Bruner 1997
WA	1996–1997	74	Multiple captures checking for brood-patch presence	Perfito 1998
AB	1997–1999	52	Telemetry and observational data	MacCallum and Godslave 2000
AB	1997–1999	88	Telemetry	Smith 2000
Labrador	1999–2001	92	Splayed pelvis, sunken abdomen; egg in oviduct	Goudie and Jones 2005

proportions of nonbreeding females likely include some failed nesters and late nesters and, hence, breeding propensity often may be underestimated (McFarlane Tranquilla et al. 2003).

We quantified breeding propensity of female harlequin ducks by applying 2 methods, yolk precursor analyses and radiotelemetry, which are targeted at 2 different stages of reproduction. Yolk precursor measurements indicated breeding propensity based on the proportion of captured females that were in the process of egg production. Plasma yolk precursors, vitellogenin (VTG) and yolk-targeted, very-low-density lipoprotein (VLDLy), are produced in the avian liver and become elevated as estrogen concentrations increase during reproduction (Deeley et al. 1975, Chan et al. 1976). Vitellogenin and VLDLy function as the primary sources of egg yolk protein and lipid, respectively (Wallace 1985, Walzem 1996). These yolk precursors are tightly coupled with follicle development because they are low during nonreproductive stages and then increase quickly and dramatically at the onset of egg production (Salvante and Williams 2002, Vézina and Williams 2003). Yolk precursors have been demonstrated to be reliable indices of reproductive status in European starlings (*Sturnus vulgaris*; Challenger et al. 2001), marbled murrelets (*Brachyramphus marmoratus*; Vanderkist et al. 2000, McFarlane Tranquilla et al. 2003), and greater scaup (*Aythya marila*; Gorman 2005). Radiotelemetry allowed us to estimate breeding propensity by determining the proportion of females that began incubation. Finding a female on a nest with radiotelemetry confirmed that she did produce eggs, although failure to detect a female on a nest did not necessarily indicate she did not produce eggs, given that lack of detection on a nest could result from either nonbreeding or early nest predation. Our objective was to compare the efficiency of each method for estimating breeding propensity and to derive an overall estimate of breeding propensity that accounts for misclassification of breeding status by each method.

STUDY AREA

We captured harlequin ducks on streams in the southern Coast Mountains of British Columbia, Canada, from 9 May to 20 May 2003 and from 21 April to 20 May 2004 using mist nets. The study area included the following streams near the towns of Lillooet (50°41′N, 121°56′W) and Pemberton (50°19′N, 122°48′W): Bridge River, Seton River, Cayoosh Creek, Yalakom River, Ryan River, Rutherford Creek, and Brandywine Creek.

Also, we captured wintering ducks from 27 February to 11 April 2004 in the Strait of Georgia, British Columbia, using a floating mist-net capture method adapted for inshore ocean use (Kaiser et al. 1995). Capture locations were around Hornby Island (49°31′N, 124°42′W), Denman Island (49°32′N, 124°49′W), and Qualicum Bay (49°24′N, 124°38′W). Some harlequin ducks from these wintering areas are known to breed near Lillooet and Pemberton (J. C. Bond, unpublished data).

METHODS

We immediately removed captured birds from the net, and then weighed, banded, and assigned them to an age class based on the depth of the Bursa of Fabricius (Mather and Esler 1999). Research methods were approved by the Simon Fraser University Animal Care Committee (permit no. 668B-033). On the breeding grounds, we attached a radiotransmitter to each captured female using a subcutaneous anchor and glue (Pietz et al. 1995). The transmitters (Holohil Systems Ltd., Carp, ON, Canada) were a 6-g, RI-2B model with a motion-sensitive mortality sensor and a battery life of 3–9 months. We monitored radiotagged females at least once per week (usually several times per week) to determine if each female was on a nest. We classified those on nests as breeders and those not on nests as putative nonbreeders. We also categorized some individuals as unknown if their radio signal was lost during the nesting period.

We took a 1.5-mL blood sample from the jugular veins of captured females using a heparinized 5.0-mL syringe with a 21-gauge needle. For some females, we used a 1.0-mL syringe with a 24-gauge needle to take 0.5 mL of blood from the tarsal vein instead. We transferred collected blood to a heparinized vial and stored it on ice until the plasma was separated from cellular blood components using a centrifuge (within 12 hr of collection). We analyzed plasma for yolk precursor concentrations of VTG and total VLDL (both generic and yolk-targeted). We used diagnostic kits for vitellogenic zinc and total triglycerides as indices of concentrations of VTG and VLDL, respectively (Mitchell

and Carlisle 1991, Williams and Christians 1997). Intra-assay and inter-assay coefficients of variation for VTG were 3.2% and 13.0% ($n = 6$) and for VLDL were 5.1% and 4.3% ($n = 5$), respectively. We analyzed plasma samples from females captured on wintering grounds in the Strait of Georgia, British Columbia, to determine a baseline, non-breeding value for the yolk precursors ($n = 16$).

Both yolk precursors are correlated with egg production; however, VTG has been shown to be a more accurate and reliable indicator of reproductive status than VLDL (Vanderkist et al. 2000, Gorman 2005). Therefore, we considered VTG first for determining whether females were captured during egg production. Although yolk precursors are very low in nonbreeding birds, we determined conservative cut-off levels for breeding and nonbreeding classifications (Salvante and Williams 2002, Vézina and Williams 2003). We categorized individual females into 1 of 3 categories based on VTG results: egg producing, non–egg producing, and unknown. The unknown category included females whose VTG concentration fell within a range we considered uncertain. The lower limit of this uncertain zone was the mean VTG of our wintering females + 3 standard deviations (0.44 μg/mL), as recommended by McFarlane Tranquilla et al. (2003). Because 0.44 μg/mL is low compared to other values in the literature, we also used an upper limit for the unknown category, which was the highest cut-off value reported in the literature (1.4 μg/mL; Gorman 2005). We considered any individuals with VTG values >1.4 μg/mL to be egg producers (hence breeders) and we categorized those <0.44 μg/mL as non–egg producers and putative nonbreeders. If we categorized an individual as unknown based on VTG level, we then used VLDL value to evaluate status. As with VTG, we also used VLDL values to categorize these birds as egg producers, non–egg producers, or unknown with the lower limit defined as mean VLDL + 3 standard deviations for our wintering females (3.66 mg/mL) and the upper limit of 5.2 mg/mL from published literature (Gorman 2005). If we classified a female as unknown for both VTG and VLDL, then we considered her overall breeding status using yolk precursors unknown.

Our summary dataset for estimation of breeding propensity consisted of classifications of breeder, putative non-breeder, or unknown for each individual for each of our 2 methods, using yolk precursors as a measure of egg production and radiotelemetry to infer egg production from birds detected on nests. We estimated a putative breeding propensity for each method individually as simply the proportion of individuals that were classified as breeders, excluding those classified as unknown from the calculation. Because we were using 2 methods to estimate breeding propensity, we also calculated a misclassification rate for each method, which was the proportion of birds that were incorrectly classified as a putative nonbreeder when it was known to produce eggs based on the other method. We multiplied the misclassification rates for each method to estimate the probabil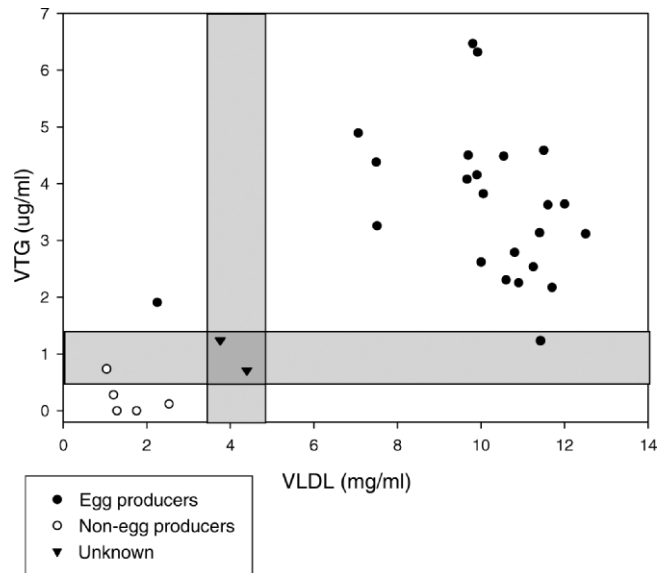ity of incorrectly designating an individual as a nonbreeder when using both methods. The product of the misclassification rates estimated the proportion of birds that were truly breeders but that were captured before the onset of rapid follicle growth and that their nest failed before telemetry methods confirmed incubation. An overall estimate of breeding propensity was the proportion of individuals confirmed as a breeder by either method plus the estimate for the proportion misclassified as a nonbreeder by both methods.

Figure 1. Yolk precursor data for breeding propensity determination for female harlequin ducks capture in the southern Coast Mountains of British Columbia, Canada, in 2003 and 2004. The yolk precursors displayed are vitellogenin (VTG) and very-low-density lipoprotein (VLDL). Symbols show how we classified each individual based on yolk precursor cut-off criteria and grey areas are zones of uncertainty determined by lower and upper cut-off values for breeding and nonbreeding individuals. Note 2 individuals only had values for VTG and, therefore, are not shown.

RESULTS

Over the 2 years of our study, we captured and radiotagged 34 female harlequin ducks on breeding streams (15 in 2003 and 19 in 2004). We determined that the age class of all captured females was after third year (i.e., breeding-age ad). We captured and monitored 5 females in both years and included data for both years in analyses.

The 2 methods we applied produced different estimates for breeding propensity. Yolk precursor analyses showed that of the 34 females, 25 were producing eggs when captured (8 of 15 in 2003; 18 of 19 in 2004; Fig. 1). Five were not producing eggs, 2 were classified as unknown because their values fell within the uncertain zone for both yolk precursors, and 2 had blood samples that were unusable for analyses. Therefore, we estimated a putative breeding propensity based solely on yolk precursors to be 83%. Our telemetry efforts resulted in detection of 22 females on nests (9 of 15 in 2003; 13 of 19 in 2004), 8 females that were never found on nests, and 4 whose status was unknown (due to loss of radio signal or mortality); therefore, putative breeding propensity using telemetry was 73%. Using both

F captured on streams	Egg producers based on yolk precursors	Egg producers based on radiotelemetry	
34	Yes — 25	Yes — 17	
		Unk — 3	
		No — 5	
	Unk — 4	Yes — 4	
		No — 0	
	No — 5	Yes — 1	
		Unk — 1	
		No — 3	

Figure 2. Breeding-propensity classification for 34 female harlequin ducks we captured on streams in the southern Coast Mountains of British Columbia, Canada, in 2003 and 2004. Determination of egg producers and non–egg producers (Unk = unknown) is based on breeding activity at 2 points in the reproductive cycle (i.e., yolk precursors measure egg production and radiotelemetry measures incubation). This figure illustrates how each method can be used separately and in conjunction to determine number of females that initiated egg formation.

data types combined, we designated 3 females on breeding streams as putative nonbreeders, one was unknown, and we confirmed by ≥1 method that 30 (91%) had initiated egg production. However, this estimate does not include those breeding females that could have been missed by both methods.

Misclassification rates differed by method. Using radio-telemetry alone, we would have misclassified 17% of egg producers as nonbreeders. Of the 30 females categorized by telemetry, 5 putative nonbreeders were known to be breeders based on yolk precursors (Fig. 2). These 5 egg producers presumably failed early during the nesting phase before we could detect them on nests via telemetry. Yolk precursor analysis was less likely to misclassify breeders as putative nonbreeders. Of the 30 birds with yolk precursor data indicating their breeding status, only one (3%) was classified as a putative nonbreeder based on yolk precursors but which we subsequently confirmed to produce eggs based on telemetry (Fig. 2). This was a late-nesting bird that presumably we captured prior to rapid follicle growth. Our estimate of the proportion of individuals misclassified by both methods, derived by multiplying misclassification rates of each method used independently, was low (1%), indicating that it was unlikely for both methods to miss a breeding bird. Our final estimate of breeding propensity (proportion of known breeders by either method plus the estimate of misclassification by both methods) was 92%. The 2 years of data showed similar results, with breeding-propensity estimates of 86% and 95% for 2003 and 2004, respectively.

DISCUSSION

Our estimate of breeding propensity for adult female harlequin ducks in southern British Columbia (92%) is notably high compared to previous estimates. Speculation of low breeding propensity by harlequin ducks originated in Iceland where Bengtson and Ulfstrand (1971) suggested that there are generally a high proportion of female harlequin ducks on breeding streams each year that are nonbreeders. Since then there have been variable estimates obtained using differing techniques (Table 1). As discussed by Cam et al. (1998), the criteria used to distinguish between breeding and nonbreeding individuals can have an important influence on study results and conclusions. Most approaches used for harlequin ducks have methodological constraints and cannot distinguish between true nonbreeders and females that fail early in the egg production or incubation stages, which has likely resulted in estimates that are lower than true breeding propensity.

Although our comparatively high estimate of breeding propensity could be a site or year effect, we suspect it is more likely a function of the methods we used. To accurately determine breeding propensity, it is important to measure egg production rather than infer it at a later reproductive stage. There are new and improving techniques that measure the occurrence of egg production. Lindstrom et al. (2006) recently suggested measuring postovulatory follicles in mallards as a means of determining egg production and, hence, breeding propensity. Plasma yolk precursor analysis, which we used, is a nonlethal measure of egg production and recent studies have improved our understanding of VTG and VLDLy dynamics (Challenger et al. 2001, Salvante and Williams 2002, Vézina and Williams 2003, Gorman 2005). Further research in this area could lead to a direct measure of egg production, rather than relying on indices.

Further, using 2 methods directed at different phases of the reproductive cycle is useful in that it allows estimation of misclassification rates by each method as well as calculation of an estimate of overall misclassification. For yolk precursor analysis, if a female is caught during ovarian follicle development, her status as an egg producer will be evident because yolk precursor levels increase rapidly with onset of rapid follicle growth and decrease rapidly as soon as the last follicle is ovulated (Challenger et al. 2001, Vézina and Williams 2003, Gorman 2005). However, if a female is caught outside of the egg production stage, yolk precursors cannot distinguish nonbreeders from those that will initiate egg formation later or have already completed egg laying. Our estimate of misclassification when using yolk precursors was surprisingly low (3%), indicating that our captures were well timed. Radiotelemetry misclassified females that began egg production but failed before we could detect the nest during incubation. It is likely that early nest loss is responsible for much of this misclassification. Both methods together resulted in a low overall misclassification rate and allowed accurate estimates of breeding propensity.

Our high breeding-propensity estimate does not support

the idea that there are generally a high proportion of nonbreeders on breeding streams (Bengtson and Ulfstrand 1971) nor that harlequin ducks, although they are a long-lived species, are quick to defer breeding to increase survival and lifetime reproductive success (Stearns 1992, Goudie et al. 1994). Estimates of breeding propensity of common eiders (*Somateria mollissima*), another long-lived sea duck, averaged around 75% with incidents as low as 45% (Coulson 1984). Also, breeding propensity of greater snow geese (*Chen caerulescens*) has been reported to average around 57% (Reed et al. 2004). Our estimate of harlequin duck breeding propensity, which is high relative to other long-lived species and suppositions for harlequin ducks in the literature, may indicate that their life-history strategy is not as extreme as previously suggested or that the years of our study were particularly favorable for initiating reproduction. In either case, harlequin ducks in our study did not appear to be strongly constrained in their ability to produce eggs. Applying our methods across a range of conditions for harlequin ducks would give a more comprehensive view of breeding propensity and, hence, life-history strategies and management implications.

Breeding propensity is a rarely investigated, but informative, demographic parameter that has been shown to be useful for understanding factors influencing population declines and low productivity. Peery et al. (2004) included breeding propensity when considering limiting factors, such as food, nest sites, or predation, on marbled murrelet populations. Also, Reed et al. (2004) found that spring snow cover negatively influenced breeding propensity and, therefore, productivity of greater snow geese. For harlequin ducks, Bengtson and Ulfstrand (1971) suggested that low food availability can reduce productivity by lowering breeding propensity. Most recently, Goudie and Jones (2005) concluded that productivity for harlequin ducks in Labrador was limited by predation rather than food availability, based on activity budgets and high breeding-propensity estimates. However, conclusions for harlequin ducks based on breeding-propensity estimates in previous studies should be considered with caution because of issues concerning methodologies (see above). Conditions prior to reproduction, on wintering or spring staging areas, also could affect breeding propensity, and these cross-seasonal effects have become increasingly recognized as potentially important (Tamisier et al. 1995, Webster et al. 2002, Bond and Esler 2006). Research addressing cross-seasonal effects on breeding propensity would be challenging but exceedingly valuable.

Management Implications

We reiterate that accurate estimates of breeding propensity are important for determining factors that influence reproductive success and productivity and subsequent population dynamics. Low breeding propensity may be indicative of a physiological influence such as poor nutrient availability, whereas a high proportion of breeding females that fail to complete incubation indicates that external factors such as high predation pressure dictate productivity.

Harlequin ducks in our study exhibited high breeding propensity suggesting that they were not limited in their ability to produce eggs. Therefore, management action to increase productivity should be focused on enhancing other reproductive stages such as nest and brood survival. Additional evaluations of breeding propensity of harlequin ducks, across an array of breeding areas, would be useful to determine the ubiquity of our findings and, thus, of our management implications.

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