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COMMENTARY

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DEMOGRAPHY, GENETICS, AND THE VALUE OF MIXED MESSAGES

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Abstract. Iverson et al. (2004) used estimates of the homing rate for molting adult Harlequin Ducks (*Histrionicus histrionicus*) in Alaska to draw inferences about population structure. Homing rates, defined as one minus the ratio of birds recaptured elsewhere to those recaptured at the original banding site, were high (0.95–1.00) for males and females. Iverson et al. (2004) concluded that these high rates of homing are indicative of demographic independence among molting groups separated by small distances (tens to hundreds of kilometers) and that conservation efforts should recognize this fine-scale population structure. We re-examined their use of the homing rate, because their assumption of equal detection probability across a wide sampling area could have led to an upward bias in their estimates of site fidelity. As a result, we are hesitant to agree with their conclusion of high adult homing to molting areas and that molt-site fidelity is evidence for demographic independence. Our hesitancy stems from the fact that little is known about juvenile and adult movements within and among years, breeding area origins, and the variation of demographic parameters (e.g., survival and productivity) among molting groups. Furthermore, population genetic data of these molting groups suggest gene flow at both nuclear and mitochondrial loci. Such mixed messages between demographic (i.e., banding) and genetic data are increasingly common in ornithological studies and offer unique opportunities to reassess predictions and make more robust inferences about population structure across broad temporal and spatial scales. Thus, we stress that it is this broader scale perspective, which combines both demography and genetics, that biologists should seek to quantify and conservation efforts should seek to recognize.

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Key words: *Harlequin Duck,* Histrionicus histrionicus*, homing rate, population structure, winter philopatry.*

Demografía, Genética y el Valor de los Mensajes Confusos

Resumen. Iverson et al. (2004) usaron estimaciones de la tasa de retorno de individuos mudando a adultos de *Histrionicus histrionicus* en Alaska para inferir la estructura poblacional de esta especie. Las tasas de retorno, definidas como uno menos el cociente entre las aves recapturadas en otro lado y aquellas recapturadas en el sitio original de anillado, fueron altas (0.95–1.00) tanto para machos como para hembras. Iverson et al. (2004) concluyeron que estas tasas de retorno indican que existe independencia demográfica entre los grupos de muda que están separados por cortas distancias (decenas a centenas de kilómetros) y que los esfuerzos de conservación deben reconocer esta estructura poblacional a pequeña escala. Re-examinamos el uso de la tasa de retorno debido a que la suposición de los autores de que existe una misma probabilidad de detección a través de una vasta área de muestreo podría haber generado un sesgo positivo en sus estimaciones de fidelidad de sitio. Como resultado de esto, cuestionamos sus conclusiones de que existe un elevado retorno de los adultos a las áreas de muda y de que la fidelidad a los sitios de muda es evidencia de independencia demográfica. Nuestra inseguridad surge del hecho de que se conoce poco sobre los movimientos de los juveniles y adultos adentro y entre años, sobre los orígenes de las áreas reproductivas y sobre la variación de los parámetros demográficos (e.g., supervivencia y productividad) entre los grupos de muda. Más aún, los datos de genética poblacional de estos grupos sugieren que existe flujo génico tanto en los loci nucleares como mitocondriales. Estos mensajes confusos entre los datos demográficos (i.e., anillado) y genéticos son cada vez más comunes en los estudios ornitológicos y ofrecen oportunidades únicas para re-evaluar las predicciones y establecer inferencias más robustas sobre la estructura poblacional considerando amplias escalas temporales y espaciales. De este modo, resaltamos que es esta perspectiva más amplia, que combina demografía y genética, la que deben cuantificar los biólogos y reconocer los esfuerzos de conservación.

Structured genetic and demographic patterns are predicted for species that exhibit high levels of natal philopatry (Avise 2004:499). Such patterns are not predicted when natal philopatry is low, even if adults are site faithful, because juvenile dispersal and

subsequent reproduction will lead to gene flow among populations (Cabe 1999, Lovette et al. 2004, Arsenault et al. 2005). Yet several molecular examinations of avian species presumed to exhibit natal philopatry (Ransom et al. 2001, Roeder et al. 2001, Kimura et al. 2002, Pearce et al. 2004), or those documented to exhibit high levels of natal philopatry through banding studies (Avise et al. 1992, Birt-Friesen et al. 1992, Austin et al. 1994), have found sampled populations to be largely homogeneous at neutral genetic loci. These mixed messages arise for two general and nonmutually exclusive reasons: differences in the scale of measurement, and dispersal that results in gene flow.

First, demographic (i.e., banding) and genetic data assess patterns across very different geographic and temporal scales, thus mixed messages are not restricted to avian taxa (Tallmon et al. 2002, Hauswaldt and Glenn 2005). Genetic methods infer dispersal via gene flow over much larger geographic scales than is usually possible with banding data. Furthermore, no genetic estimates of dispersal are truly contemporary, but rather represent an average rate of gene flow across multiple generations up to some point in the recent past (Bossart and Prowell 1998). Thus, historical events, such as those related to post-Pleistocene ice movements (Hewitt 2000), can create a condition whereby insufficient time has elapsed since range expansions for natal philopatry to result in genetic differences among populations (Slatkin 1987, Avise 2004). Second, juvenile dispersal and subsequent reproduction results in gene flow among populations (Cabe 1999, Frederiksen et al. 2002, Arsenault et al. 2005). As a result, numerous authors have argued for a combined, multimarker approach to quantify historical and ongoing factors to best infer population patterns (Avise et al. 1992, Bossart and Prowell 1998, Koenig et al. 2000, Kimura et al. 2002, Kendall and Nichols 2004).

Mixed messages have recently confronted researchers investigating molting and wintering groups of Harlequin Ducks (*Histrionicus histrionicus*) in Alaska and British Columbia. Lanctot et al. (1999) used mitochondrial (mt) DNA control region sequence data and nuclear microsatellite loci to characterize molting groups of Harlequin Ducks in southcentral Alaska. Results suggested that sampling areas were largely homogeneous for both types of genetic markers, although slightly higher levels of differentiation were observed between more distant regions using mtDNA. This result was surprising as Cooke et al. (2000) observed adult Harlequin Ducks to exhibit high levels of site fidelity to molting and wintering areas of coastal British Columbia, which they suggested could lead to genetic differentiation of wintering aggregations if mate choice occurs in these locations. Following many years of intensive study, Iverson et al. (2004) were able to quantify between-year rates of adult molt-site fidelity of Harlequin Ducks in Prince William Sound, Alaska via the homing rate. They observed high homing rates (0.95–1.0) and concluded that these estimates are indicative of demographic independence among molting groups at a finer scale than indicated by genetic data.

Here, we re-examine the homing rate estimator used by Iverson et al. (2004), their conclusion that high male and female adult homing rates are indicative of demographic independence, and offer a review of the distinction between demographic and genetic population structure. One note on terminology: we feel the word 'philopatry' does not adequately apply to nonbreeding areas and that a species is philopatric only if dispersal is limited with respect to an organism's natal area (Greenwood 1980, Shields 1982). Therefore, because Harlequin Ducks in Prince William Sound do not breed where they molt, we use the term 'adult molt-site fidelity' instead of winter philopatry, since Iverson et al. (2004) were concerned with the return of adults to molting areas.

DEMOGRAPHY

Iverson et al. (2004) captured and marked molting Harlequin Ducks throughout Prince William Sound, Alaska from 1995 to 1997 and 2000 to 2001. Adult males and females were marked with standard metal leg bands. Hatch-year birds were capable of flight and thus unavailable for capture and marking. Banding data were analyzed using an estimator of homing rate, which Iverson et al. (2004:712) define as "the ratio of birds recaptured on their original capture site to those recaptured elsewhere (Robertson and Cooke 1999)." This definition of homing rate differs from that given by Anderson et al. (1992), which includes an estimation of fidelity (F), temporary emigration (γ), and recapture (p) given presence. It also differs from the return rate (R), which includes an estimation of survival (S) as well as F, γ, and p (Williams et al. 2002). These estimators can be biased due to confounding among the various parameters, but the direction of the bias is known because noncapture probabilities are estimated. Thus, for the homing rate of Iverson et al. (2004) to accurately quantify fidelity, all marked birds must be recaptured with the same probability regardless of their subsequent molting location (i.e., p cannot vary between birds that return and those that disperse). In other words, the homing rate estimator

$$\mathrm{SF}p_1/(\mathrm{S}[\mathrm{F}p_1 + (1 - \mathrm{F})p_2]),$$

where S drops out, cannot simplify to F unless $p_1 = p_2$. Iverson et al. (2004) acknowledged this assumption and used multiple 'supplementary sites' to document any dispersal events away from the primary Montague Island sites. However, given the fact that most dispersal events detected by Iverson et al. (2004) were of short distances (3.1–8.9 km), our prediction is that dispersal events to supplementary sites >8.9 km should have a lower p than those within 8.9 km of the primary capture locations. Additionally, the longest dispersal event documented via recapture was 51.9 km. Therefore, all Harlequin Ducks within 51.9 km of their initial capture location must have the same probability of recapture following dispersal as those that do not disperse for the assumption of equal capture probability to be met. Thus, the assumption of equal p across Prince William Sound may not have been appropriate and a lower p

for supplementary sites may have resulted in an overestimate of the homing rate at primary sites.

Knowledge of several aspects of movement ecology would enhance the characterization of molt-site fidelity in Harlequin Ducks, such as the distribution of molting birds along Montague Island. Do unsampled molting flocks that could contain marked birds occur close to the three primary sampling areas? What is the number of birds banded at time t, not observed at time $t + 1$, but subsequently observed at time $t + i$? Such data would provide information on detection probabilities, movements among molting sites, and the timing of molt migrations. Also, what is known about the timing of molt for nonbreeding versus brood-rearing females? Are nonbreeding and successfully breeding females equally available for capture during molt drives? Cooke et al. (2000) observed that both younger and older males move among areas and that winter site fidelity may be contingent upon the availability of unpaired females or territoriality of paired males. Thus, information on the number, sex, and age of unbanded birds captured by Iverson et al. (2004) is of interest. Such information seems necessary to fully evaluate the conclusion of Iverson et al. (2004) that molting flocks exhibit high site fidelity and are demographically independent. Demographic independence implies that each molting group is characterized by unique rates of survival and reproduction. If solely males move among molting groups, there is the possibility that population structure exists among females, but nothing is known about the location of breeding areas of female Harlequin Ducks that molt and winter throughout Prince William Sound. Furthermore, low levels of differentiation among females for maternally inherited mtDNA (see below) suggest that movement among molting areas is not strictly limited to males. In the absence of such information, it is unclear how adult male and female homing rates are indicative of unique demographic and thus conservation units at such a small scale.

GENETICS

Behavioral traits of waterfowl have led to various hypotheses about the location and degree of population genetic structure. First, in most waterfowl species females exhibit greater natal and breeding site fidelity than males (Greenwood 1980, Anderson et al. 1992). Over sufficient periods of time and spatial scale, natal philopatry can lead to genetic differentiation, especially at maternally inherited molecular loci such as mtDNA. Second, both sexes may exhibit winter site fidelity for a variety of ecological and genetic reasons, including re-establishment of breeding pairs as mate choice is thought to occur on the wintering grounds (reviewed by Robertson and Cooke 1999). In either case adult nest or winter site fidelity might also serve to differentiate populations, but only at larger scales where populations are separated at distances greater than all dispersal events. However, even at these larger scales, genetic differentiation can be limited by historical demographic processes and large effective population sizes, which reduces the diversifying forces of mutation and drift (reviewed by Avise 2004).

In Harlequin Ducks, molt-site fidelity would only lead to demographic and population genetic structure if molting flocks remain as distinct units throughout the entire year. Regehr et al. (2001) observed that Harlequin Duck broods may accompany adult females to molting sites. However, it is not known if juvenile Harlequin Ducks, especially females, return to these same molting areas as adults in subsequent years. Tracking natal dispersal of birds via mark-recapture methods is very difficult because efforts must be made to recapture previously marked individuals across a wide range of possible dispersal distances. This difficulty is compounded among sea duck species, which typically do not breed until their second or third year. Thus, data from multiple years and wide geographical efforts would be needed to discern the range of possible dispersal events (Lebreton et. al. 2003). However, if dispersal is male-biased, one might predict higher levels of population differentiation using maternally inherited mtDNA in contrast to nuclear DNA, which tracks both maternal and paternal lineages. Lanctot et al. (1999) observed precisely this pattern, with slightly elevated levels of differentiation for mtDNA in comparison to nuclear microsatellite data among regional groupings of female Harlequin Ducks. Still, the level of mtDNA differentiation observed by Lanctot et al. (1999) was low ($\Phi_{ST} = 0.05$) suggesting some female gene flow, but at a reduced level compared to males.

Cooke et al. (2000) viewed the genetic data of Lanctot et al. (1999) as validation of their conclusions of male-mediated gene flow, but Iverson et al. (2004) found the genetic data unable to "indicate" the fine-scale population structure suggested by the homing rate. First, little is known about the breeding area origins of molting Harlequin Ducks in Prince William Sound. Genetic data would only indicate fine-scale structure if each molting flock remained isolated throughout the year and over thousands of generations. A more likely scenario is that each molting flock is composed of birds from multiple breeding areas. Second, consider the genetic implications of demographic independence on such a fine scale. If juveniles follow females to molting sites each year and then both sexes continually return to those sites each year at a homing rate of 0.95–1.0 (Iverson et al. 2004), two immediate predictions for these flocks are: (1) elevated levels of inbreeding within each "demographically independent" molting flock, and (2) substantially higher levels of mtDNA population differentiation due to the smaller effective population size of mtDNA compared to nuclear loci and the small size of each molting flock ($n \sim 30$), compounding genetic drift. Neither of these predictions is borne out by Lanctot et al. (1999). Genotype data from five microsatellite loci showed no significant heterozygote deficiencies, inbreeding coefficients did not differ significantly from zero, and levels of population differentiation estimated using mtDNA were low.

Other hypotheses concerning the population genetics of wintering Harlequin Ducks in Prince

William Sound include: (1) a lack of power among genetic markers to distinguish wintering groups, (2) insufficient time since populations expanded into northern latitudes for site fidelity patterns to accrue genetic differences, and (3) molt-site fidelity is a complex behavioral process. A lack of power seems unlikely because fewer genetic loci have shown population differentiation in other waterfowl that exhibit high levels of adult site fidelity (Pearce et al. 2000). Harlequin Ducks have likely experienced historical population growth and expansion since the last glacial maximum. Consistently low levels of nucleotide diversity (near zero) across populations, as observed by Lanctot et al. (1999), are indicative of sudden population growth and expected if time is sufficient for recovery of haplotype variation via mutation, but too short for the accumulation of differences among sequences (reviewed by Avise 2000). Lastly, Lanctot et al. (1999) correctly acknowledged that movements of subadult birds among molting sites before patterns of adult fidelity are established might nullify the effects of high adult fidelity to these same sites (as observed in other species; Cabe 1999, Arsenault et al. 2005). No increase in DNA samples or genetic loci would recover a signal of population differentiation if natal and adult dispersal occur among these molting groups. Such movements would also erode any demographic independence among these same groups.

The hypothesis of molt or winter site fidelity leading to demographic and genetic structure deserves further examination because anthropogenic effects on sea duck populations often occur on the wintering grounds (Flint et al. 1999, Esler et al. 2000, Camphuysen et al. 2002). However, recent work suggests little genetic evidence for population structure among wintering sea ducks at either regional (Lanctot et al. 1999) or continental scales (Pearce et al. 2004). Additionally, the literature presented by Iverson et al. (2004) does not support a hypothesis that strong affiliations to nonbreeding areas are common among sea duck species. Papers by Alison (1974) and Savard (1985) are each based upon a single marked bird, and Limpert (1980) estimated a homing rate of 39%. Of 26 male and two female Harlequin Ducks banded by Breault and Savard (1999), nine males were seen at the same location in the following year, while two males were seen at an adjacent molting site. Thus, this and other literature (Cooke et al. 2000, Flint et al. 2000, Hatton and Marquiss 2004, Mehl et al. 2004) suggests that annual affiliations to molting areas by sea ducks are quite variable. Lastly, we view molt-site fidelity as a less than robust measure of population structure without evidence that molting flocks originate from distinct breeding areas. Under the scenario that molting flocks are composed of birds from a variety of breeding areas, fidelity is instead an intriguing behavioral pattern and not a measure of demographic independence.

THE VALUE OF MIXED MESSAGES

Conservation plans often seek to delineate geographic or taxonomic units as distinct population segments to effectively monitor status and trends (U.S. Fish and Wildlife Service and National Marine Fisheries Service 1996). Defining such units relies upon a wide array of criteria that for migratory birds may include morphological or plumage characteristics, demographic patterns quantified by banding or radio-telemetry, molecular genetic data, or geographic separation of population segments during the annual cycle. However, focusing on only one type of data to define such units misdirects valuable research and conservation efforts (Zink et al. 2000) and tends to promote population structure as a binary condition: populations are either structured or they are not (Crandall et al. 2000). A larger set of direct and indirect markers are now available for assessing movement patterns (reviewed by Webster et al. 2002, Kendall and Nichols 2004), as well as novel analytical methods that *estimate* levels, directionality, and sources of variation in dispersal rather than simply *testing* dispersal as a binary condition (Pritchard et al. 2000, Hey and Nielsen 2004, Kendall and Nichols 2004). Thus, we wish to stress that behavioral patterns among avian populations are intricate and idiosyncratic (Avise et al. 1992, Zink et al. 2003, Coltman 2004), and efforts should focus on the robust quantification of these multifaceted processes with as much information as possible.

For example, a number of avian genetic studies discuss the impact of historical demographic processes on levels of population differentiation and the need for other, nongenetic data to verify or challenge conclusions (Bossart and Prowell 1998, Kimura et al. 2002, Pearce et al. 2005). Similarly, banding studies have called for DNA-based estimates of movement after recognizing the difficulty of detecting and quantifying long-distance dispersal (Koenig et al. 2000, Arsenault et al. 2005). In a joint analysis of banding and genetic data for the Lesser Snow Goose (*Anser caerulescens*), Avise et al. (1992:1094) argued appropriately that "both evolutionary (genetic) and contemporary (behavioral) perspectives are required for a full appreciation of the geographic population structure of a species."

An examination of the table of contents of recent ornithological and molecular ecology journals reveals the current focus on demographic parameters (e.g., nesting success, productivity, survival, dispersal, and colonization history) and their role in population status and trends. Yet a common misconception is that genetic data are a panacea for inferring population structure. Instead, molecular genetic markers should be viewed as offering a singular but multifaceted perspective on population differentiation and demography. Regardless of whether genetic or nongenetic methods are used, we encourage researchers to use multiple data types when they are available. Even in cases where genetic data suggest no differentiation among sampling locales, such as among molting groups of Harlequin Ducks, there is still a wealth of information that can be inferred from the molecular information, such as historical population trends (Emerson et al. 2001), geographic variation in genetic diversity (Busch et al. 2000, Zink et al. 2000), relative levels of female natal philopatry and male dispersal (Pearce et al. 2005), or evidence

for gene flow via dispersal that is difficult to assess with localized banding data (Arsenault et al. 2005). Because inferences from multiple markers reveal the weaknesses and strengths of each method, comparisons among data types provide a competing model framework to reassess predictions, evaluate temporal and spatial scales, and best infer population patterns.

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