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Quantifying partial migration with sex-ratio balancing

Haley A. Ohms^{1,*}

Alix I. Gitelman²

Chris E. Jordan³

Dave A. Lytle¹

1. Department of Integrative Biology, Oregon State University, Corvallis, Oregon 97331;

2. Department of Statistics, Oregon State University, Corvallis, Oregon 97331;

3. Northwest Fisheries Science Center, National Oceanic and Atmospheric Administration, Seattle, Washington 98112

* Corresponding author; e-mail: haley.ohms@gmail.com

+ Current address: Institute of Marine Sciences, University of California Santa Cruz; and Southwest Fisheries Science Center, National Oceanic and Atmospheric Administration, Santa Cruz, California 95062

Abstract

Partial migration, the phenomenon in which animal populations are composed of both migratory and non-migratory individuals, is widespread among migrating animals. The proportion of migrants in these populations has direct influences on population genetics and dynamics, ecosystem dynamics, mating systems, evolution, and responses to environmental change, yet there are very few studies that measure the proportion of migrants. This is because existing methods to estimate the proportion of migrants are time-consuming and expensive. In this paper, we demonstrate a new method for estimating the proportion of migrants in a population, based on sex-ratio measurements. Many partially migratory taxa exhibit sex-biased migration or residency, and in these cases, the sex ratios of migrants and non-migrants are fundamentally related to the proportion of migrants in the population. We define this relationship quantitatively and show how it can be used to infer the proportion of migrants in a population through a process we term ‘sex-ratio balancing.’ We obtain Bayesian estimates of proportion of migrants, and quantify the uncertainty in these estimates with highest posterior density intervals. Lastly, we validate the sex-ratio balancing approach with a Chinook salmon (*Oncorhynchus tshawytscha* Walbaum, 1792) data set. Sex-ratio balancing holds promise as a tool for quantifying partial migration and filling a key data gap about partially migratory taxa.

Key words

Partial migration, sex-ratio balancing, sex ratio, female-biased migration, Chinook salmon, *Oncorhynchus tshawytscha*, life-history diversity

Introduction

Life-history diversity is recognized as an important mechanism for population

persistence, stability, and resilience (Kerr et al. 2010; Schindler et al. 2010). One particularly dramatic form of life-history diversity is the co-occurrence of migratory and non-migratory individuals, or 'partial migration' (Lack 1944). Partial migration was originally described in birds (Lack 1944), but has since been documented in over 60 species of birds, bats, insects, fish, ungulates, amphibians, and reptiles (Table 1). It occurs in marine, freshwater, and terrestrial habitats, and can range from several thousand kilometer migrations in salmonid fishes (Larsen et al. 2013) to single kilometer elevational migrations in birds (Morrissey 2004) and bats (Senior et al. 2005). Despite the strong interest and considerable research on the mechanisms that might lead to such life-history diversity, there are surprisingly few estimates of the partial migration at the population-level.

Most of the research on partial migration focuses on the mechanisms that might lead to migration and residency life histories by comparing individual differences, such as growth performance or lipids (McMillan et al. 2012; Sloat et al. 2014), or fitness trade-offs (Grayson et al. 2011). Other studies have focused on how natural selection maintains the two phenotypes using theoretical models (Kokko 2007, 2011; Taylor and Norris 2007; Lundberg 2013), or genetic effects (Pearse et al. 2014). Each of these studies makes predictions about the proportion of migrants in a population and how that proportion should respond to changes in the environment. For example, if the density of newts in a pond increases, growth declines through density-dependent competition, fitness trade-offs change, and the proportion of migrants in a population should increase (Grayson et al. 2011). Yet, the proportion of migrants and non-migrants in populations is rarely measured, and in studies where it is measured, the measurement is typically made in only one year and one population (exceptions are L'Abée-Lund et al. 1990; Morita and Nagasawa 2010; Sahashi and Morita 2013), which makes testing

predictions about responses to environmental change impossible. The lack of this fundamental information stands as a significant gap in our understanding of population dynamics and ecosystem processes; it limits the ability to test ecological and evolutionary hypotheses and it can result in management strategies that are poorly informed about this population characteristic. This knowledge gap, however, is not a problem of oversight, but rather due to the difficulties in collecting appropriate data.

Methods that have been most successful in producing estimates for the proportion of migrants are (a) tagging and tracking and (b) lethal sampling. Tagging/tracking includes capturing individuals, tagging them and tracking them to determine their life history outcome (Rabenold and Rabenold 1985; Rikardsen and Elliott 2000; White et al. 2007; Hebblewhite et al. 2008; Cagnacci et al. 2011; Mysterud et al. 2011; Bai et al. 2012; Gaidet and Lecomte 2013; Perez et al. 2013). This method is both time consuming and expensive, it is limited to relatively large organisms, and tags can have a limited functioning life. As a result, studies generally track relatively few individuals (fewer than 100). Lethal sampling involves collecting individuals and identifying those that are maturing and will not migrate. It has been used in some salmonids (L'Abee-Lund et al. 1990; Morita and Nagasawa 2010; Sahashi and Morita 2013); however, it is limited to taxa in which mature non-migrants and migrants co-occur, and those for which permits can be obtained for lethal sampling. Isotopic signatures have been used to determine behavior using fish otoliths (Tsukamoto et al. 1998; Secor et al. 2001; Fukumori et al. 2008; Gillanders et al. 2015) and using bird feathers (Perez et al. 2013). This method, however, misses the individuals that undertook migration or residency and died, and otolith sampling is lethal. Proxies for migration have also been used (e.g., the presence or absence of marine parasites on fish; Kristoffersen et al. 1994), but proxies are system-specific and assessing their accuracy is

difficult. These collective methodological challenges hinder our ability to quantify partial migration over large spatial and temporal scales, and they demonstrate the need for a more cost- and time-efficient method.

One solution to this problem is to identify a characteristic of the population that may be related to migration proportion and that is easier to measure. One such characteristic is sex ratios, though the connection to migration proportion is perhaps not intuitive. Many partially migratory populations exhibit sex-biased patterns of migration or residency. In most of these populations, females are more likely than males to migrate, but there are also some cases in which males are more likely to migrate (Table 1). Female-biased migration is attributed to the different energetic requirements for reproduction in males and females. Females require more energy for reproduction (Trivers and Willard 1973; Fleming 1996; Hendry and Berg 1999; Fleming and Reynolds 2004; Hayward and Gillooly 2011), and migration often provides access to habitats with greater food resources (Albon and Langvatn 1992; Cote et al. 2004; Hendry and Stearns 2004; Hebblewhite and Merrill 2011; Bai et al. 2012; Rolandsen et al. 2016), therefore more females than males migrate. Likewise, when non-migration provides better food resources, more females than males will be non-migrant (Swingland and Lessells 1979; Nicholson et al. 1997). Sex-biased migration acts as a constraint on the population composition because there are a limited number of males and females that can be divided into migrants and non-migrants. Because of this constraint, if the sex ratios of the two phenotypes and the proportion of females in the population are known, the ratio of migrants to non-migrants can be inferred.

In this paper, we define the relationship between female-biased partial migration and the proportion of migrants. We call this relationship ‘sex-ratio balancing,’ and we demonstrate how it can be used to estimate the proportion of migrants. We use a Bayesian estimation

approach and quantify uncertainty using a highest posterior density intervals. Lastly, we demonstrate the utility of sex-ratio balancing with a Chinook salmon data set.

The Conceptual Model

Consider a population of partial migrants in which migrant and non-migrant adults have offspring that become either migrant or non-migrant. The sex ratio at birth is assumed to be 1:1 (male : female), and because we assume no sex-specific mortality from birth to the juvenile stage, the sex ratio of juveniles is also 1:1. Some fraction of the juveniles become migrants and the remainder become non-migrants. The fraction that migrates is female biased (Table 1). Note that we use the female-biased migration as an example throughout the paper, but the same logic could be applied to male-biased migration. We again assume there is no sex-specific mortality at the transition from juvenile to migrant or non-migrant (note, this assumption can be relaxed in the θ parameter described in the next section). Although there is now sex bias in the migrant and non-migrant phenotypes, the population-level sex ratio remains at 1:1. Because there are finite numbers of males and females in each group, the sex bias in each group, and the relative proportion of the population assigned to each group, are related.

This relationship is illustrated in Figure 1 using three scenarios. Each of the three scenarios begins with a 1:1 juvenile sex ratio. The proportion of the population assigned to the non-migrant and migrant groups is different in each scenario (as indicated by the size of a circle), but the migrant sex ratio remains constant (i.e., 1:3). Because the relative proportion assigned to the non-migrant and migrant groups changes in each scenario, the non-migrant sex ratios are forced to change. It is this relationship between the sex ratios and proportion of migrants that allows us to infer the proportion of migrants from sex ratios.

Sex-ratio balancing

We transform that conceptual model into a quantitative relationship, first by defining the following parameters:

$$\varphi_m : \quad \text{Proportion of migrants in the population } (0 \leq \varphi_m \leq 1) \quad (1)$$

$$f_m : \quad \text{Proportion of migrants that are female } (0 \leq f_m \leq 1) \quad (2)$$

$$f_n : \quad \text{Proportion of migrants that are female } (0 \leq f_n \leq 1) \quad (3)$$

$$\theta : \quad \text{Proportion of migrants that are female } (0 \leq \theta \leq 1) \quad (4)$$

Notice that if we assume the population sex ratio is 1:1 at birth and that there is no sex-specific mortality, then the sex ratio remains 1:1 at the population level. In this case, we can take $\theta = 0.5$ in (4), even though females and males may adopt different migrant and non-migrant tactics. At this point for generality, however, we do not make this simplifying assumption.

Using basic rules of probability,

$$\theta = f_m \varphi_m + f_n (1 - \varphi_m), \quad (5)$$

and then solving (5) for φ_m we have:

$$\varphi_m = \frac{\theta - f_n}{f_m - f_n}. \quad (6)$$

Equation (6) shows that the proportion of migrants in a population is a function of the proportions of females (equivalently, males) in the population and in the two subpopulations—migratory and non-migratory. The importance of this relationship lies with the sex ratios. Sex ratios are less time consuming and less expensive to measure than tagging and tracking individuals or conducting a mark-recapture study. Because of the relationship in (5), there are some constraint on f_m , f_n and θ . Specifically, one of

$$f_n < \theta < f_m \quad (7)$$

$$f_m < \theta < f_n \quad (8)$$

must hold. Notably, the inequalities in (7) and (8) must strictly hold for sex-ratio balancing to be an effective method for estimating the migratory proportion, φ_m .

Sex-ratio balancing highlights the constraints among the proportion migrants, the sex ratio of migrants, the sex ratio of non-migrants, and the overall sex ratio (Figure 2). For a given population-level sex ratio (θ), there is only one φ_m for a pair of f_m and f_n values.

Correspondingly, any migrant sex ratio greater than 0.5 can be associated with a non-migrant sex ratio between 0 and 0.5, but φ_m necessarily changes.

Before describing the details of our Bayesian approach to estimating φ_m , we discuss a generalization of (6) that allows for different migration tactics depending upon age, and we highlight how sex-ratio balancing can be used to answer two subtly different questions.

In the conceptual model and Figure 1, we presented a population with a 1:1 sex ratio at birth, juveniles transition to migrant or non-migrant, and the overall population sex ratio remains 1:1. This allows us to estimate the proportion of migrants in a single cohort (i.e., birth year). The same logic that works for a cohort also applies to a population in a single year. If we know the population-level sex ratio prior to migration and residency, and we know the rates of sex-specific mortality prior to migration or residency (if there is any), we can use sex-ratio balancing to estimate the proportion of migration in the population in a single year. This is true regardless of the ages, prior migratory behavior, or prior reproduction. In other words, sex-ratio balancing in the form given in equation (5) gives the proportion migrant of a population or cohort in a single year. If the question one hopes to answer is what is the proportion migration from a single cohort in a particular year (i.e., “what proportion of migration took place for the 1983 cohort at age-2?”), the equation (5) must be adjusted slightly and additional data collection

is necessary.

Addition of age structure

In equations (5) and (6), we made the simplifying assumption that the transition from birth to migration or residency takes place at the same age. In many taxa, however, this transition takes place over multiple years. For example, in one study of partially migratory steelhead and rainbow trout, individuals became migrants or non-migrants between one and five years of age (Ohms et al. 2013). If one seeks to find the proportion of migrants from a single cohort, in a single year, then we must relax this assumption. To explore the consequences of relaxing this assumption, we create a two-stage model in which a fraction of individuals transitions to migrant, non-migrant, or deferral in year one, and another fraction transitions to migrant or non-migrant in year two (Figure 3). This framework could be expanded to include more ages, but for the purposes of demonstration we use only two ages.

The following model applies to one cohort of organisms, where a cohort is defined as having the same birth year. For the first year in which these individuals *could* migrate, we take:

- φ_{m1} : Proportion of year-1 migrants in the cohort ($0 \leq \varphi_{m1} \leq 1$)
- f_{m1} : Proportion of year-1 migrants that are female ($0 \leq f_{m1} \leq 1$)
- f_{n1} : Proportion of year-1 non-migrants and deferrals that are female ($0 \leq f_{n1} \leq 1$)
- θ_1 : Proportion of females in the cohort in year 1 ($0 \leq \theta_1 \leq 1$)

This component of the model replicates the model in equations (1) through (4) above because this is simply the first year that the individuals in the cohort can migrate. And as before, we can write φ_{m1} using the relationship:

$$\varphi_{m1} = \frac{\theta_1 - f_{n1}}{f_{m1} - f_{n1}}.$$

Once we move to the second year, the overall proportion of females from the cohort must

be adjusted to reflect that males and females may have migrated differentially in the first year.

To this end, we must estimate:

$$\varphi_{m2} : \quad \text{Proportion of year-2 migrants in the cohort } (0 \leq \varphi_{m2} \leq 1) \quad (9)$$

$$f_{m2} : \quad \text{Proportion of year-2 migrants that are female } (0 \leq f_{m2} \leq 1) \quad (10)$$

$$f_{n2} : \quad \text{Proportion of year-2 non-migrants that are female } (0 \leq f_{n2} \leq 1) \quad (11)$$

$$\theta_2 : \quad \text{Proportion of year-1 non-migrants that are female } (0 \leq \theta_2 \leq 1) \quad (12)$$

It is important to note that sex-based differences in mortality from year one to year two can be accounted for by recognizing that θ_2 is the proportion of cohort females available to migrate in year two.

Again using the basic rules of probability, we can write φ_{m2} using

$$\varphi_{m2} = \frac{\theta_2 - f_{n2}}{f_{m2} - f_{n2}},$$

and then substituting f_{n1} for θ_2 :

$$\varphi_{m2} = \frac{f_{n1} - f_{n2}}{f_{m2} - f_{n2}} \quad (13)$$

As in the case with only a single year of migration, here, with two years of migration to consider, we only need to measure sex-ratios to get an estimate of the proportion of individuals that migrate. This multiple year migration can be perpetuated, by again using sex-ratios in subsequent years.

Bayesian modeling approach

We return to the single cohort model in (6) to complete a Bayesian specification and describe our model fitting approach. The sex ratios that contribute to θ , f_m and f_n must be estimated from data. As such, they will be estimated with uncertainty that propagates to the estimate of the proportion migrating, φ_m . In our approach, we assign prior distributions to θ , f_m

and f_n , and use Bayesian updating to obtain draws from the posterior distribution of each of these parameters. Then, we obtain draws from the posterior distribution of φ_m by combining the posterior draws of θ , f_m and f_n using equation (6). We then report a 95% highest posterior density interval (HDP) for φ_m . We use a HPD interval rather than an equal tailed posterior interval to avoid any potential issues with asymmetric posteriors (Gelman et al. 2013). We formalize our model as follows:

$$X_m \sim \text{Binomial}(N_m, f_m) \quad (14)$$

$$X_n \sim \text{Binomial}(N_n, f_n) \quad (15)$$

where N_m and N_n are the sample sizes available for estimating f_m and f_n , respectively. We assign bounded uniform priors for f_m and f_n , conditional on θ :

$$f_m|\theta \sim \text{Uniform}(\theta, 1) = \frac{1}{1-\theta}, \text{ for } f_m \in [\theta, 1] \quad (16)$$

$$f_n|\theta \sim \text{Uniform}(0, \theta) = \frac{1}{\theta}, \text{ for } f_n \in [0, \theta] \quad (17)$$

These bounded priors reflect the constraints in equations (7) and (8). Female-biased migration is the most commonly observed bias among partially migratory species (1), though these priors can also be used to reflect a male-biased dispersal or migration pattern by assigning prior distributions of $f_m|\theta \sim \text{Uniform}(0, \theta)$ and $f_n|\theta \sim \text{Uniform}(\theta, 1)$. Furthermore, if prior data were available, we could incorporate it in (16) and/or (17).

For the overall population sex ratio, θ , we assume an existing binomial observation, and can assume either an informed or a relatively non-informative prior for θ . In the case where we have data to create an informed prior, the prior is:

$$Y \sim \text{Binomial}(N, \theta) \quad (18)$$

$$\theta \sim \text{Beta}(\alpha, \beta) \quad (19)$$

where α and β are the parameters of the Beta distribution (Gelman et al. 2013). In the case where we have no data for a prior, we assume:

$$Y \sim \text{Binomial}(N, \theta) \quad (20)$$

$$\theta \sim \text{Beta}(49.5, 49.5) \quad (21)$$

This prior, the Beta(49.5,49.5) distribution, has a mean equal to 0.5 and standard deviation of 0.05. While it's unlikely that the population sex ratio is exactly 0.5, it's also very unlikely that it's wildly different from 0.5, and this prior reflects this. In cases where a population sex ratio cannot be estimated (i.e., there is no available data), the prior distribution for θ can still be used to produce posterior estimates for the migration proportion.

We calculate the posterior distribution of the parameter vector (θ, f_m, f_n) using Bayes theorem, and we sample from this joint posterior distribution using a Gibbs Sampler (e.g., Gelman et al. 2013, p. 276) constructed in R (R Core Team 2017). The full conditional distributions of θ, f_m , and f_n are each truncated Beta distributions, so the Gibbs sampler is straightforward. Details of this calculation, as well as example R code, are provided in supplementary material. Finally, by combining the posterior draws of θ, f_m , and f_n using (6), we obtain draws from the posterior distribution of φ_m .

The 95% HPD interval for φ_m is the set of values, C , satisfying,

$$\int_C f(\varphi_m | X_m, X_n, Y) d\varphi_m = 0.95 \quad (22)$$

Such that any value $\varphi_m \in C$ and any value $\varphi_m^* \notin C, f(\varphi_m | X_m, X_n, Y) \geq f(\varphi_m^* | X_m, X_n, Y)$, where $f(\varphi_m | X_m, X_n, Y)$ denotes the posterior distribution of φ_m given the data. The R code to generate HPD intervals is included in supplementary material.

Validation in Chinook Salmon

We used a study on Chinook Salmon (*Oncorhynchus tshawytscha* Walbaum, 1792) conducted by Harstad et al. 2014 to validate sex-ratio balancing for the single-cohort case. This study was well suited for validating sex-ratio balancing because the Chinook salmon were raised in hatcheries, which are a closed system, and make it relatively easy to measure the proportion of migrants and the migrant and non-migrant sex ratios. Chinook are also well suited to validate sex-ratio balancing because in certain populations known as ‘stream-type Chinook’ salmon both migrants and non- migrants spend one year in freshwater before migrating to the ocean as migrants, or maturing in freshwater as non-migrants (Healey 1991).

Chinook salmon are notable, although not completely unique, in that males can be migrant or non-migrant, but all females migrate (Healey 1991; Harstad et al. 2014; Table 1). This makes sex-ratio balancing slightly simpler in that the proportion of female non-migrants is equal to zero, which simplifies equation 5 to:

$$\varphi_m = \frac{\theta}{f_m} \quad (23)$$

The HPD calculation also changes slightly because f_n is zero in the calculation (R code included in supplementary material).

Harstad et al. 2014 collected stream-type Chinook salmon from five hatcheries between 2008 and 2011, although not all hatcheries were sampled in every year (Figure 4). They collected approximately 300 fish from each hatchery, in each sample year, and measured the number of females, the number of males, and the number of non-migrant males (i.e., the males undergoing sexual maturation). We used these data to calculate the initial sex ratio (θ), the migrant sex ratio (f_m), and the non-migrant sex ratio (f_n). Based on those values, we calculated the median proportion of migrants and a 95% HPD interval using sex-ratio balancing,

and compared that to the measured proportion of migrants and a 95% frequentist confidence interval.

We found that the proportion of migrants estimated by sex-ratio balancing was not always identical to the measured proportion of migrants; however, the HPD interval always included the measured proportion of migrants (Figure 4). The HPD intervals were wider than the confidence intervals, and in general they more often included a proportion migrant equal to one. When the proportion of migrants was greater than 0.9 sex-ratio balancing was close to the measured proportion of migrants. However, when the measured proportion of migrants was lower than 0.9, sex-ratio balancing over-estimated the value. This likely has to do with the uniform priors on f_m and f_n , which could be adjusted to reflect new information.

Discussion

Quantifying the proportion of migrants in partially migratory species is critical for understanding population dynamics and the ecological and evolutionary processes that drive this life history diversity. In this paper, we present the first formally defined quantitative relationship between migrant and non-migrant sex ratios and the proportion of migrants. We demonstrate how this relationship can be leveraged to infer the proportion of migrants through sex-ratio balancing. Sex-ratio balancing can be applied to a variety of organisms that inhabit a wide range of habitats (Table 1), and has explicit, testable assumptions.

A key benefit of sex-ratio balancing is that it uses sex ratio data, which can usually be collected in a non-lethal manner, and is often collected concurrently with other data (i.e., Senior et al. 2005; Grayson and Wilbur 2009; Perez et al. 2013). Researchers have used a variety of non-lethal sex determination methods that include visual identification (Senior et al. 2005), morphological measurements (Perez et al. 2013), vocalization identification (Perez et al.

2013), ultrasound (Bonar et al. 1989), and genetic identification (Ohms et al. 2013). These non-lethal methods are especially important for species protected by the U.S. Endangered Species Act, or other laws, and whose sample availability may be considerably restricted. In addition, sex identification is generally far less time-consuming and expensive than the alternative methods of tagging and tracking individuals, isotope analysis, or comparing the numbers of migrants and non-migrants.

One concern with regards to sex-ratio balancing is sex-specific mortality. It is well documented that sex-specific mortality can arise during reproduction (Adler and Bonduriansky 2011; Grayson et al. 2011), because of differences in age-of-reproduction (Carlson et al. 2004), and during or after migration itself (Thompson et al. 2016). Sex-specific mortality influences sex-ratio balancing only in time-frame prior to the initial sex ratio measurement, when θ is estimated. This can be in the juvenile stage if using sex-ratio balancing for a single cohort, or it can be the time-frame just prior to migration and residency if using sex-ratio balancing for a population in a single year. Therefore, if sex ratios can be measured just prior to or immediately after the transition from juvenile to migrant or non-migrant, any sex-specific mortality that takes place later in life will not influence the estimated proportion of migrants. It will not be feasible to measure sex ratios just prior to or immediately after the transition from juvenile to migrant or non-migrant in all populations or situations, and this should be considered prior to using sex-ratio balancing.

Another important consideration is that sex-ratio balancing will not be an appropriate method in all situations. There will be cases in which not all assumptions can be met, and these must be considered carefully when applying sex-ratio balancing. For example, the case may arise in which multiple partially migratory populations having overlapping migratory

habitat. The non-migrant sex ratios for each population can be measured, but measuring the migrant sex ratios may be more challenging because migrants from the multiple populations are mixed. It is possible that the populations may have different migratory propensities (ϕ_m), as well as different proportions of migrants that are female (f_m). In this case, sex-ratio balancing should only be used if the proportions of migrants that are female (f_n) can be measured in each population prior to mixing with the other populations. If the f_m cannot be measured for each population separately, sex-ratio balancing will not be an accurate method for estimating the proportion of migrants in each population.

We validated sex-ratio balancing by applying it to populations in which the proportion of migrants was measured directly (Harstad et al. 2014). We found that the median proportion of migrants estimate differed slightly from the measured estimate, however the measured value was always within the 95% HPD interval. That sex-ratio balancing did not achieve exactly the same values as the direct measurement is somewhat dissatisfying, until one considers that direct measurement is often exceedingly difficult. As an example, there are numerous occasions in which people have measured the proportion of migrants in hatchery Chinook populations (Larsen et al. 2010, 2013, Harstad et al. 2014; Fast et al. 2015; Beckman et al. 2017), and only one occasion in which people have measured the proportion of migrants in a wild Chinook population (Larsen et al. 2013). The lack of measurements is not for lack of interest, but because non-migrant Chinook salmon are small, cryptic, and hard to catch, which makes quantifying the proportion of migrants a real challenge. This lack of information has real consequences for Chinook salmon management and conservation. There is growing concern that Chinook salmon hatcheries are producing an unnatural amount of non-migrants because the proportion of non-migrants is, in some cases, as high as 30% (Figure 4). However, with

such little data, we do not know whether 30% is outside of the normal range for wild populations, and whether or not hatcheries should change their practices to decrease the number of non-migrants they produce. Sex-ratio balancing provides a tool that can address this important data gap.

The lack of data on the proportion of migrants has consequences for management and conservation in other partially migratory species beyond Chinook salmon (Table 1). Knowing the basic population demographics, such as the proportion of migrants, is critical for setting restoration goals, prioritizing habitat conservation and movement corridors, predicting susceptibility to climate change, and assessing harvest consequences (Brenkman and Corbett 2005; McGuire and Boyle 2013; Moore et al. 2014). Sex-ratio balancing can be used to inform decisions and will hopefully improve management, conservation, and the understanding of partially migratory species in general.

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Figure Captions

Figure 1: An illustration of the relationship between migrant (mig.) and non-migrant (non.) sex ratios and the proportion of migrants and non-migrants in the population. In each of the three cases, the juvenile sex ratio is 1:1 (male:female) and the migrant sex ratio is female biased (a sex ratio of 1:3). However, as the relative proportion of migrants and non-migrants changes, the non-migrant sex ratio ranges between slightly male biased (a ratio of 3:2) to extremely male biased (a ratio of 9:1). The migrant and non-migrant sex ratios mirror each other only when the proportion of migrants and non-migrants is equal (50%).

Figure 2: The relationship between the proportion of migrants and sex ratios in the migrant and non-migrant groups, assuming $\theta = 0.5$ (equation 6). This surface is limited to the case of female-biased migrants and male-biased non-migrants.

Figure 3: Life cycle diagrams based on the (I) simple model with no age structure (equation 6) and (II) model with two ages (equation 13). In (I) juveniles (j) become migrant (m_1) or non-migrant (n_1) in the same year. In (II), juveniles (j) can defer their 'decision' to migrate for one year and become deferral (d_1), migrant (m_2) or non-migrant (n_2) in the second year. In year-1 we can estimate the proportion of migrants, but the estimated proportion of year-1 non-migrants ($1 - \phi_{m1}$) includes both non-migrants and deferrals. These are denoted with the dotted grey line. This combination is a mathematical necessity, but also biologically relevant in that non-migrants and deferrals are often indistinguishable at this stage, unless identified by lethal sampling.

Figure 4: The proportion of migrants in five hatchery populations of Chinook salmon (*Oncorhynchus tshawytscha* Walbaum, 1792) measured by Harstad et al. 2014, compared to the proportion of migrants calculated by sex-ratio balancing. Sample sizes are relatively similar for

all years (i.e., they range from 294-302). Error bars on the measured proportions are 95% frequentist confidence intervals, and are 95% Bayesian HPD intervals on the sex-ratio balancing proportions.

Draft

Figures

Figure 1

Figure 2

Figure 3

Figure 4

Table 1: Review of Known Partially Migratory Taxa and Sex-Specific Differences in Behaviour

Species	Source	Migrants	Non-migrants
Birds			
Cory’s Shearwater (<i>Calonectris Diomedea</i> Scopoli, 1769)	Perez et al. 2013	equal	male biased
House Finch (<i>Carpodacus mexicanus</i> P. L. Statius Müller, 1776)	Able and Belthoff 1998	equal	equal
American Dipper (<i>Cinclus mexicanus</i> Swainson, 1827)	Gillis et al. 2008	unknown	unknown
White-ruffed Manakin (<i>Corapipo altera</i> Hellmayr, 1906)	Boyle 2008	equal	equal
European Robin (<i>Erithacus rubecula</i> Linnaeus, 1758)	Adriaensen and Dhondt 1990	uniquely female to female biased	uniquely male to male biased
Dark-eyed Junco (<i>Junco hyemalis</i> Linnaeus, 1758)	Rabenold and Rabenold 1985	female biased	male biased
Great Bustards (<i>Otis tarda</i> Linnaeus, 1758)	Alonso et al. 2000	equal	equal
Blue Tit (<i>Cyanistes caeruleus</i> Linnaeus, 1758)	Smith and Nilsson 1987	uniquely female	male biased
Willow Tit (<i>Poecile montanus</i> Conrad von Baldenstein, 1827)	Silverin et al. 1989	equal	equal
Goldcrest (<i>Regulus regulus</i> Linnaeus,	Hildén 1982	equal to female biased	equal to male biased

1758)

Blackcap (<i>Sylvia atricapilla</i> Linnaeus, 1758)	Pérez-Tris and Tellería 2002	female biased	male biased
European Blackbird (<i>Turdus merula</i> Linnaeus, 1758)	Lundberg 1985	female biased	male biased
Tropical Kingbird (<i>Tyrannus melancholicus</i> Vieillot, 1819)	Jahn et al. 2010	female biased	male biased
Lanyu Scops Owl (<i>Otus elegans botelensis</i> Kuroda, 1928)	Bai et al. 2012	unknown	male biased
European Shags (<i>Phalacrocorax aristotelis</i> Linnaeus, 1761)	Grist et al. 2017	equal	equal

Reptiles

Aldabra Tortise (<i>Aldabrachelys gigantea</i> Schweigger, 1812)	Swingland and Lessells 1979	male biased	female biased
Giant Tortise (<i>Chelonoidis nigra</i> Quoy and Gaimard, 1824)	Blake et al. 2013	equal	equal

Amphibian

Red-spotted newt (<i>Notophthalmus viridescens</i> Rafinesque, 1820)	Grayson and Wilbur 2009	female biased	male biased
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Mammals**Ungulates**

Impala (<i>Aepyceros melampus</i> Lichtenstein, 1812)	Gaidet and Lecomte 2013	equal	equal
Moose (<i>Alces alces</i> Linnaeus, 1758)	Ball et al. 2001	unknown	unknown

Pronghorn (<i>Antilocapra americana</i> Ord, 1815)	White et al. 2007	unknown	unknown
Bison (<i>Bison bison</i> Linnaeus, 1758)	Bruggeman et al. 2008	unknown	unknown
Roe deer (<i>Capreolus capreolus</i> Linnaeus, 1758)	Mysterud 1999	uniquely female	male biased
Red deer (<i>Cervus elaphus</i> Linnaeus, 1758)	Mysterud et al. 2011	unknown	unknown
Elk (<i>C. canadensis</i> Erxleben, 1777)	Hebblewhite et al. 2008	unknown	unknown
Sika deer (<i>C. nippon</i> Temminck, 1838)	Takii et al. 2012	even	even
Blue Wildebeest (<i>Conochaetes taurinus</i> Burchell, 1823)	Morrison and Bolger 2012	unknown	unknown
Mule Deer (<i>Odocoileus hemionus</i> Rafinesque, 1817)	Nicholson et al. 1997	male biased	uniquely female
White-tailed deer (<i>O. virginianus</i> Zimmermann, 1780)	Van Deelen et al. 1998	equal	equal
Tibetan Antelope/Chiru (<i>Pantholops hodgsonii</i> Abel, 1826)	Schaller 1998	unknown	unknown
Reindeer (<i>Rangifer tarandus platyrhynchus</i> Linnaeus, 1758)	Hansen et al. 2010	unknown	unknown
African buffalo <i>Syncerus caffer</i> Sparrman, 1779)	Naidoo et al. 2012	unknown	unknown
Bats			
Daubenton's bat (<i>Myotis daubentonii</i> Kuhl, 1817)	Senior et al. 2005	uniquely male	female biased

Insects

Common Green Darner (<i>Anax junius</i> Drury, 1773)	May 2013	unknown	unknown
Southern Monarch (<i>Danaus erippus</i> Cramer, 1775)	Slager and Malcolm 2015	unknown	unknown

Fish

Common bream (<i>Abramis brama</i> Linnaeus, 1758)	Skov et al. 2011	unknown	unknown
Black bream (<i>Acanthopagrus butcheri</i> Munro, 1949)	Gillanders et al. 2015	equal	equal
Shortnose sturgeon (<i>Acipenser brevirostrum</i> Lesueur, 1818)	Altenritter et al. 2017	unknown	unknown
European eel (<i>Anguilla anguilla</i> Linnaeus, 1758)	Tsukamoto et al. 1998	equal	equal
Spotnape cardinalfish (<i>Apogon notatus</i> Houttuyn, 1782)	Fukumori et al. 2008	equal	equal
Atlantic herring (<i>Clupea harengus</i> Linnaeus, 1758)	Ruzzante et al. 2006	unknown	unknown
Northern pike (<i>Esox lucius</i> Linnaeus, 1758)	Engstedt et al. 2010	unknown	unknown
Cod (<i>Gadus morhua</i> Linnaeus, 1758)	Cote et al. 2004	unknown	unknown
Three-spined stickleback (<i>Gasterosteus aculeatus</i> Linnaeus, 1758)	Kitamura et al. 2006	unknown	unknown
Humpback chub (<i>Gila cypha</i> Miller, 1946)	Yackulic et al. 2014	unknown	unknown

White perch (<i>Morone americana</i> Gmelin, 1789)	Kerr et al. 2009	equal	male biased
Striped bass (<i>M. saxatilis</i> Walbaum, 1792)	Secor et al. 2001	equal	male biased
Cutthroat trout (<i>Oncorhynchus clarkii</i> Richardson, 1836)	Trotter 1989	equal	equal
Masu salmon (<i>O. masu</i> Brevoort, 1856)	Morita et al. 2014	female biased to uniquely female	uniquely male
Rainbow trout/Steelhead (<i>O. mykiss</i> Walbaum, 1792)	Ohms et al. 2013	female biased	male biased to equal
Sockeye Salmon (<i>O. nerka</i> Walbaum, 1792)	Quinn 2005	equal	uniquely male
Chinook Salmon (<i>O. tshawytscha</i> Walbaum, 1792)	Larsen et al. 2013	female biased	uniquely male
European smelt (<i>Osmerus eperlanus</i> Linnaeus, 1758)	Jonsson and Jonsson 1993	unknown	unknown
European perch (<i>Perca fluviatilis</i> Linnaeus, 1758)	Skov et al. 2008	unknown	unknown
Zulega (<i>Prochilodus argenteus</i> Spix and Agassiz, 1829)	Godinho and Kynard 2006	unknown	unknown
Spotted sorubim (<i>Pseudoplatystoma corruscans</i> Spix and Agassiz, 1829)	Godinho et al. 2007	unknown	unknown
Roach (<i>Rutilus rutilus</i> Linnaeus, 1758)	Skov et al. 2010	unknown	unknown
Atlantic salmon (<i>Salmo salar</i> Linnaeus, 1758)	Hutchings and Jones 1998	female biased	uniquely male
Brown trout (<i>S. trutta</i> Linnaeus, 1758)	Titus and Mosegaard 1992	equal	male biased

Arctic charr (<i>Salvelinus. alpinus</i> Linnaeus, 1758)	Nordeng 1983	female biased to equal	male biased to equal
Bull trout (<i>S. confluentus</i> Suckley, 1859)	Mogen and Kaeding 2005	unknown	unknown
Brook charr (<i>S. fontinalis</i> Mitchill, 1814)	Power 1980	equal	equal
White-spotted charr (<i>S. leucomaenis</i> Pallas, 1814)	Arai and Morita 2005; Morita et al. 2000	female biased to equal	uniquely male to equal
Dolly Varden (<i>S. malma</i> Walbaum, 1792)	Koizumi et al. 2006	female biased	uniquely male
Spiny dogfish (<i>Squalus acanthias</i> Linnaeus, 1758)	McFarlane and King 2003	equal	equal

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