

Quantifying partial migration with sex-ratio balancing

Haley A. Ohms, Alix I. Gitelman, Chris E. Jordan, and Dave A. Lytle

Abstract: Partial migration, the phenomenon in which animal populations are composed of both migratory and nonmigratory 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 nonmigrants 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 in Artedi, 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.

Résumé : La migration partielle, le phénomène selon lequel des populations animales sont composées d'individus migrateurs et non migrateurs, est répandue chez les animaux migrateurs. Si la proportion de migrants dans ces populations influence directement la génétique et la dynamique de la population, la dynamique des écosystèmes, les systèmes de reproduction, l'évolution et les réactions aux changements environnementaux, très peu d'études mesurent la proportion de migrants. La raison en est que les méthodes disponibles pour estimer la proportion de migrants demandent beaucoup de temps et d'argent. Nous faisons la démonstration d'une nouvelle méthode pour estimer la proportion de migrants dans une population, qui repose sur des mesures du rapport de masculinité. Chez de nombreux taxons partiellement migrateurs, la migration ou la résidence sont biaisées selon le sexe et, dans ces cas, les rapports de masculinité des migrants et non-migrants sont fondamentalement reliés à la proportion de migrants dans la population. Nous définissons quantitativement cette relation et montrons comment elle peut être utilisée pour inférer la proportion de migrants dans une population par un processus que nous appelons “équilibre du rapport de masculinité” (« sex-ratio balancing »). Nous obtenons des estimations bayésiennes de la proportion de migrants et quantifions l'incertitude de ces estimations avec des intervalles de densité postérieure les plus élevés. Enfin, nous validons l'approche d'équilibre du rapport de masculinité en utilisant un ensemble de données sur le saumon chinook (*Oncorhynchus tshawytscha* (Walbaum in Artedi, 1792)). L'équilibre du rapport de masculinité est un outil prometteur pour quantifier la migration partielle et combler une importante lacune dans les données sur les taxons partiellement migrateurs. [Traduit par la Rédaction]

Mots-clés : migration partielle, équilibre du rapport de masculinité, rapport de masculinité, migration biaisée en faveur des femelles, saumon chinook, *Oncorhynchus tshawytscha*, diversité des cycles biologiques.

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 nonmigratory 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 kilometre migrations in salmonid fishes (Larsen et al. 2013) to single kilometre 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

Received 19 January 2018. Accepted 25 June 2018.

H.A. Ohms* and D.A. Lytle. Department of Integrative Biology, Oregon State University, Corvallis, OR 97331, USA.

A.I. Gitelman. Department of Statistics, Oregon State University, Corvallis, OR 97331, USA.

C.E. Jordan. Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Newport, OR 97365, USA.

Corresponding author: Haley A. Ohms (email: haley.ohms@gmail.com).

*Present address: Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, CA 95064, USA, and Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Santa Cruz, CA 95062, USA.

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from [RightsLink](https://www.nrcresearchpress.com/cjz).

Table 1. Review of known partially migratory taxa and sex-specific differences in behavior.

Species	Source(s)	Migrants	Nonmigrants
Birds			
Cory's Shearwater (<i>Calonectris diomedea</i> (Scopoli, 1769))	Perez et al. 2014	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, 1758))	Hildén 1982	Equal to female biased	Equal to male biased
Eurasian 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 Shag (<i>Phalacrocorax aristotelis</i> (Linnaeus, 1761))	Grist et al. 2017	Equal	Equal
Reptiles			
Aldabra Giant Tortoise (<i>Aldabrachelys gigantea</i> (Schweigger, 1812))	Swingland and Lessells 1979	Male biased	Female biased
Florea Giant Tortoise (<i>Chelonoidis nigra</i> (Quoy and Gaimard, 1824))	Blake et al. 2013	Equal	Equal
Amphibian			
Eastern (<i>Notophthalmus viridescens</i> (Rafinesque, 1820))	Grayson and Wilbur 2009	Female biased	Male biased
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
American bison (<i>Bison bison</i> (Linnaeus, 1758))	Bruggeman et al. 2008	Unknown	Unknown
Western 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>Cervus elaphus canadensis</i> Erxleben, 1777)	Hebblewhite et al. 2008	Unknown	Unknown
Sika deer (<i>Cervus nippon</i> Temminck, 1838)	Takii et al. 2012	Even	Even
Blue wildebeest (<i>Connochaetes taurinus</i> (Burchell, 1823))	Morrison and Bolger 2012	Unknown	Unknown
White deer (<i>Odocoileus hemionus</i> (Rafinesque, 1817))	Nicholson et al. 1997	Male biased	Uniquely female
Mule-tailed deer (<i>Odocoileus virginianus</i> (Zimmermann, 1780))	Van Deelen et al. 1998	Equal	Equal
Tibetan antelope (chiru) (<i>Pantholops hodgsonii</i> (Abel, 1826))	Schaller 1998	Unknown	Unknown
Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i> (Vrolik, 1829))	Hansen et al. 2010	Unknown	Unknown
African buffalo (<i>Syncerus caffer</i> (Sparman, 1779))	Naidoo et al. 2012	Unknown	Unknown
Bats			
Daubenton's myotis (<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. 2018	Unknown	Unknown
European eel (<i>Anguilla anguilla</i> (Linnaeus, 1758))	Tsakamoto 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
Atlantic cod (<i>Gadus morhua</i> Linnaeus, 1758)	Cote et al. 2004	Unknown	Unknown
Threespine 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>Morone 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>Oncorhynchus masou</i> (Brevoort, 1856))	Morita et al. 2014	Female biased to uniquely female	Uniquely male
Rainbow trout/steelhead (<i>Oncorhynchus mykiss</i> (Walbaum, 1792))	Ohms et al. 2013	Female biased	Male biased to equal
Sockeye salmon (<i>Oncorhynchus nerka</i> (Walbaum in Artedi, 1792))	Quinn 2005	Equal	Uniquely male
Chinook salmon (<i>Oncorhynchus tshawytscha</i> (Walbaum in Artedi, 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

Table 1 (concluded).

Species	Source(s)	Migrants	Nonmigrants
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>Salmo trutta</i> Linnaeus, 1758)	Titus and Mosegaard 1992	Equal	Male biased
Arctic char (<i>Salvelinus alpinus</i> (Linnaeus, 1758))	Nordeng 1983	Female biased to equal	Male biased to equal
Bull trout (<i>Salvelinus confluentus</i> (Suckley, 1859))	Mogen and Kaeding 2005	Unknown	Unknown
Brook trout (charr) (<i>Salvelinus fontinalis</i> (Mitchill, 1814))	Power 1980	Equal	Equal
White-spotted char (<i>Salvelinus leucomaenis</i> (Pallas, 1814))	Arai and Morita 2005; Morita et al. 2000	Female biased to equal	Uniquely male to equal
Dolly Varden (<i>Salvelinus malma</i> (Walbaum in Artedi, 1792))	Koizumi et al. 2006	Female biased	Uniquely male
Spiny dogfish (<i>Squalus acanthias</i> Linnaeus, 1758)	McFarlane and King 2003	Equal	Equal

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 nonmigrants 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. 1989; 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 (i) tagging and tracking and (ii) 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. 2014). 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'Abée-Lund et al. 1989; Morita and Nagasawa 2010; Sahashi and Morita 2013); however, it is limited to taxa in which mature nonmigrants 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. 2014). 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.

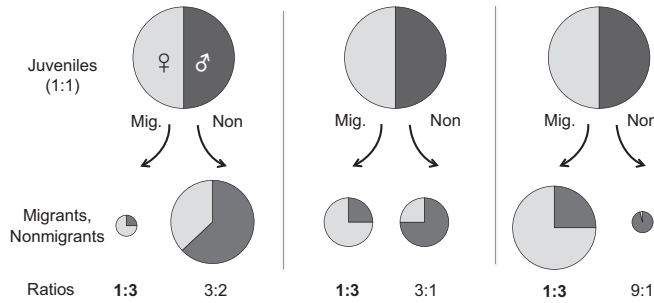
One solution to this problem is to identify a characteristic of the population that may be related to migration proportion and that is easier to measure. One such characteristic is sex ratios, although the connection to migration proportion is perhaps not intuitive. Many partially migratory populations 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. 2017); therefore, more females than males migrate. Likewise, when nonmigration provides better food resources, more females than males will be nonmigrant (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 nonmigrants. 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 nonmigrants 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 highest posterior density intervals. Lastly, we demonstrate the utility of sex-ratio balancing with a Chinook salmon (*Oncorhynchus tshawytscha* Walbaum in Artedi, 1792) data set.

The conceptual model

Consider a population of partial migrants in which migrant and nonmigrant adults have offspring that become either migrant or nonmigrant. The sex ratio at birth is assumed to be 1:1 (male to 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 nonmigrants. 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 nonmigrant (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 nonmigrant phenotypes, the population-level sex ratio remains at 1:1. Because there are finite numbers of males

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



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 Fig. 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 nonmigrant 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 nonmigrant and migrant groups changes in each scenario, the nonmigrant 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:

- (1) φ_m : Proportion of migrants in the population ($0 \leq \varphi_m \leq 1$)
- (2) f_m : Proportion of migrants that are female ($0 \leq f_m \leq 1$)
- (3) f_n : Proportion of nonmigrants that are female ($0 \leq f_n \leq 1$)
- (4) θ : Proportion of females in the population ($0 \leq \theta \leq 1$)

Notice that if we assume that 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 eq. 4, even though females and males may adopt different migrant and nonmigrant tactics. At this point for generality, however, we do not make this simplifying assumption.

Using basic rules of probability:

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

and then solving eq. 5 for φ_m , we have

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

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 nonmigratory. 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 eq. 5, there are some constraint on f_m, f_n , and θ . Specifically, one of

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

or

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

must hold. Notably, the inequalities in eqs. 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 nonmigrants, and the overall sex ratio (Fig. 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 nonmigrant 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 eq. 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 Fig. 1, we presented a population with a 1:1 sex ratio at birth, juveniles transition to migrant or nonmigrant, 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 eq. 6 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?”), eq. 6 must be adjusted slightly and additional data collection is necessary.

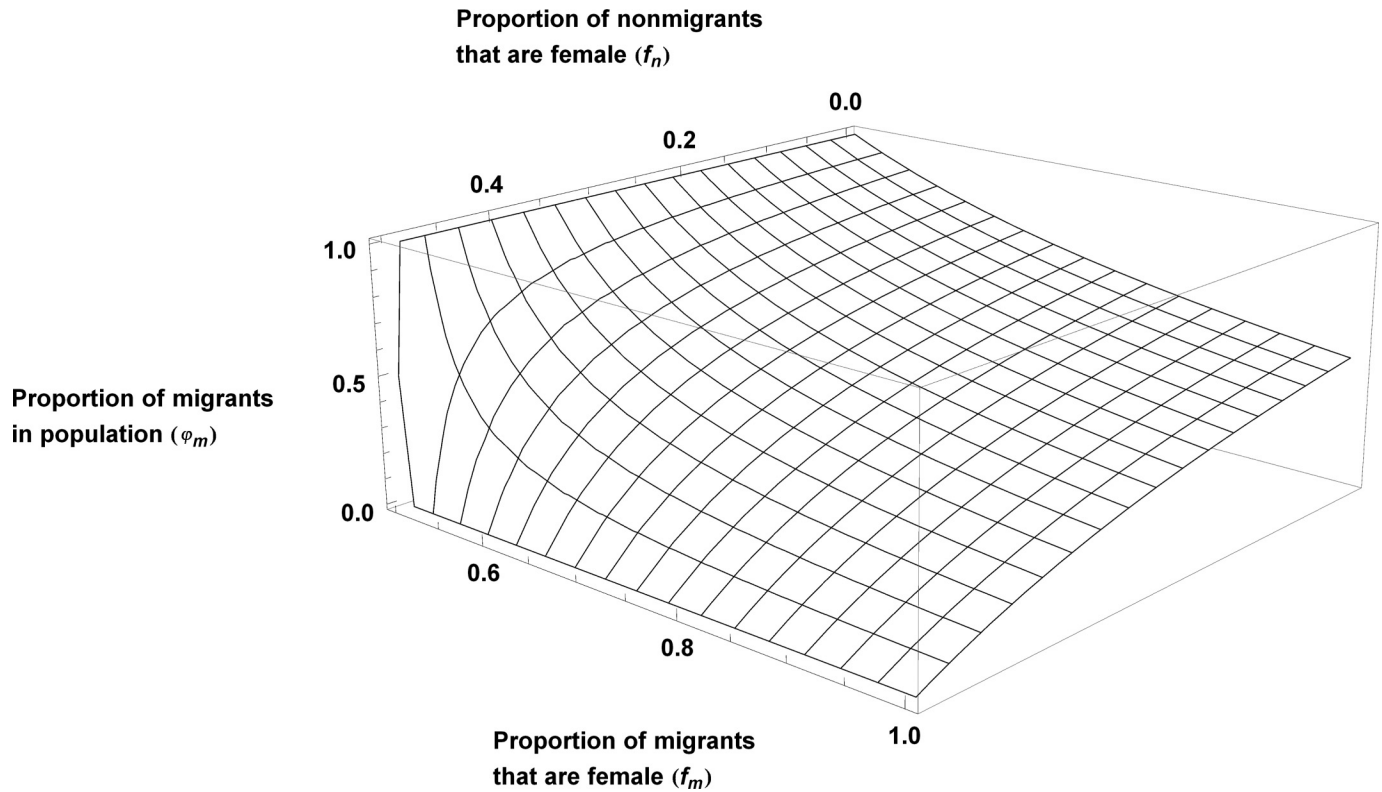
Addition of age structure

In eqs. 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 (*Oncorhynchus mykiss* (Walbaum, 1792)), individuals became migrants or nonmigrants between 1 and 5 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, nonmigrant, or deferral in year 1 and another fraction transitions to migrant or nonmigrant in year 2 (Fig. 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

Can. J. Zool. Downloaded from cdnsciencepub.com by NOAA CENTRAL on 06/05/23 For personal use only.

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



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 nonmigrants 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 eqs. 1 through 4 above because this is simply the first year that the individuals in the cohort can migrate. 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

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

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

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

(12) θ_2 : Proportion of year-1 nonmigrants that are female
($0 \leq \theta_2 \leq 1$)

It is important to note that sex-based differences in mortality from year 1 to year 2 can be accounted for by recognizing that θ_2 is the proportion of cohort females available to migrate in year 2.

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 :

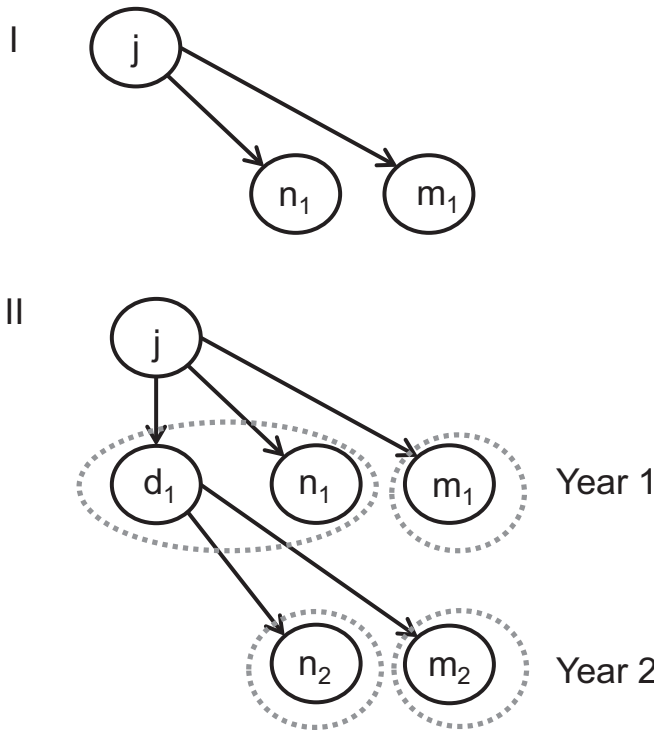
$$(13) \quad \varphi_{m2} = \frac{f_{n1} - f_{n2}}{f_{m2} - f_{n2}}$$

As in the case with only a single year of migration, here, with 2 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 eq. 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

Fig. 3. Life cycle diagrams based on the (I) simple model with no age structure (eq. 6) and (II) model with two ages (eq. 13). In I, juveniles (*j*) become migrant (*m*₁) or nonmigrant (*n*₁) in the same year. In II, juveniles (*j*) can defer their “decision” to migrate for 1 year and become deferral (*d*₁), migrant (*m*₂), or nonmigrant (*n*₂) in the second year. In year 1, we can estimate the proportion of migrants, but the estimated proportion of year-1 nonmigrants ($1 - \varphi_m$) includes both nonmigrants 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.



posterior distribution of φ_m by combining the posterior draws of θ , f_m , and f_n using eq. 6. We then report a 95% highest posterior density (HPD) interval 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:

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

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

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 :

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

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

These bounded priors reflect the constraints in eqs. 7 and 8. Female-biased migration is the most commonly observed bias

among partially migratory species (Table 1), although 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 eq. 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 noninformative prior for θ . In the case where we have data to create an informed prior, the prior is

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

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

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

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

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

This prior, the Beta(49.5, 49.5) distribution, has a mean equal to 0.5 and standard deviation of 0.05. While it is unlikely that the population sex ratio is exactly 0.5, it is also very unlikely that it is 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 material¹. Finally, by combining the posterior draws of θ, f_m , and f_n using eq. 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

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

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.

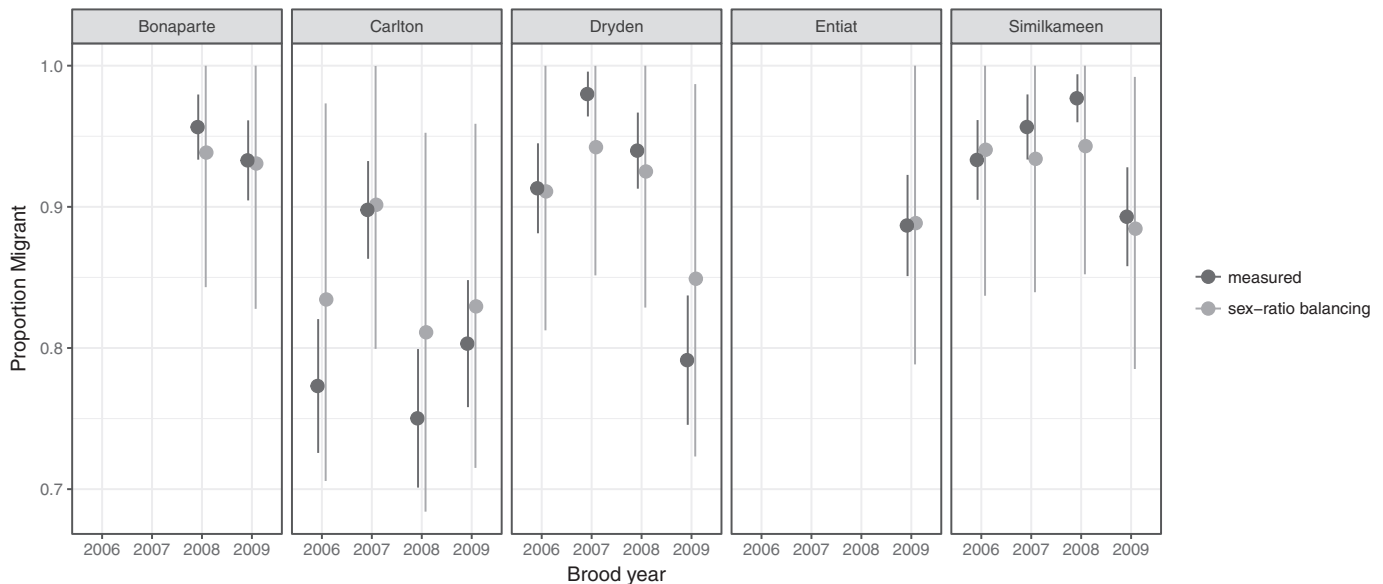
Validation in Chinook salmon

We used a study on Chinook salmon 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 nonmigrant 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 nonmigrants spend 1 year in freshwater before migrating to the ocean as migrants or maturing in freshwater as nonmigrants (Healey 1991).

Chinook salmon are notable, although not completely unique, in that males can be migrant or nonmigrant, but all females mi-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0014>.

Fig. 4. The proportion of migrants in five hatchery populations of Chinook salmon (*Oncorhynchus tshawytscha*) measured by Harstad et al. 2014 compared with the proportion of migrants calculated by sex-ratio balancing. Sample sizes are relatively similar for all years (i.e., they range from 294 to 302). Error bars on the measured proportions are 95% frequentist confidence intervals and are 95% Bayesian highest posterior density intervals on the sex-ratio balancing proportions.



grate (Healey 1991; Harstad et al. 2014) (Table 1). This makes sex-ratio balancing slightly simpler in that the proportion of female nonmigrants is equal to zero, which simplifies eq. 5 to

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

The HPD calculation also changes slightly because f_n is zero in the calculation (R code included in the 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 (Fig. 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 nonmigrant 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 nonmigrant 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 with 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 (Fig. 4). The HPD intervals were wider than the confidence intervals, and in general, they more often included a proportion migrant equal to 1. 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 overestimated 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 quan-

titative relationship between migrant and nonmigrant 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 nonlethal manner and are often collected concurrently with other data (i.e., Senior et al. 2005; Grayson and Wilbur 2009; Perez et al. 2014). Researchers have used a variety of nonlethal sex determination methods that include visual identification (Senior et al. 2005), morphological measurements (Perez et al. 2014), vocalization identification (Perez et al. 2014), ultrasound (Bonar et al. 1989), and genetic identification (Ohms et al. 2013). These nonlethal methods are especially important for species protected by the US 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 nonmigrants.

One concern with regard 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 the 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 nonmigrant, 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 nonmigrant 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 have overlapping migratory habitat. The nonmigrant 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_m) 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 the migrant 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 nonmigrant 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 nonmigrants because the proportion of nonmigrants is, in some cases, as high as 30% (Fig. 4). However, with such few 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 nonmigrants 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.

Acknowledgements

This work was funded by Bonneville Power Administration project 2003-017 and USDA Forest Service Pacific Northwest Research Station Joint Venture Agreement 13-JV-11261953-011. We appreciate the contributions of J.D. Braaten and S. de Brum on the figures, D. Larsen and D. Harstad for generously providing the Chinook data and feedback, and the thoughtful comments of two anonymous reviewers.

References

Able, K.P., and Belthoff, J.R. 1998. Rapid "evolution" of migratory behaviour in the introduced house finch of eastern North America. *Proc. R. Soc. B Biol. Sci.* 265(1410): 2063–2071. doi:10.1098/rspb.1998.0541.

- Adler, M.I., and Bonduriansky, R. 2011. The dissimilar costs of love and war: age-specific mortality as a function of the operational sex ratio. *J. Evol. Biol.* 24(6): 1169–1177. doi:10.1111/j.1420-9101.2011.02250.x. PMID:21375650.
- Adriaensen, F., and Dhondt, A.A. 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. *J. Anim. Ecol.* 59(3): 1077–1090. doi:10.2307/5033.
- Albon, S.D., and Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos*, 65(3): 502–513. doi:10.2307/3545568.
- Alonso, J.C., Morales, M.B., and Alonso, J.A. 2000. Partial migration, and lek and nesting area fidelity in female great bustards. *Condor*, 102(1): 127–136. doi:10.1650/0010-5422(2000)102[0127:PMALAN]2.0.CO;2.
- Altenritter, M.E., Zydlewski, G.B., Kinnison, M.T., Zydlewski, J.D., and Wipfelhauser, G.S. 2018. Understanding the basis of shortnose sturgeon (*Acipenser brevirostrum*) partial migration in the Gulf of Maine. *Can. J. Fish. Aquat. Sci.* 75(3): 464–473. doi:10.1139/cjfas-2017-0083.
- Arai, T., and Morita, K. 2005. Evidence of multiple migrations between freshwater and marine habitats of *Salvelinus leucomaenis*. *J. Fish Biol.* 66(3): 888–895. doi:10.1111/j.0022-1112.2005.00654.x.
- Bai, M.-L., Severinghaus, L.L., and Philippart, M.T. 2012. Mechanisms underlying small-scale partial migration of a subtropical owl. *Behav. Ecol.* 23(1): 153–159. doi:10.1093/beheco/arr168.
- Ball, J., Nordengren, C., and Wallin, K. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildl. Biol.* 7(1): 39–47. doi:10.2981/wlb.2001.007.
- Beckman, B.R., Harstad, D.L., Spangenberg, D.K., Gerstenberger, R.S., Brun, C.V., and Larsen, D.A. 2017. The impact of different hatchery rearing environments on smolt-to-adult survival of spring Chinook salmon. *Trans. Am. Fish. Soc.* 146(3): 539–555. doi:10.1080/00028487.2017.1281168.
- Blake, S., Yackulic, C.B., Cabrera, F., Tapia, W., Gibbs, J.P., Kümmeth, F., and Wikelski, M. 2013. Vegetation dynamics drive segregation by body size in Galapagos tortoises migrating across altitudinal gradients. *J. Anim. Ecol.* 82(2): 310–321. doi:10.1111/1365-2656.12020. PMID:23171344.
- Bonar, S.A., Thomas, G.L., Pauley, G.B., and Martin, R.W. 1989. Management briefs: use of ultrasonic images for rapid nonlethal determination of sex and maturity of Pacific herring. *N. Am. J. Fish. Manage.* 9(3): 364–366. doi:10.1577/1548-8675(1989)09<0364:MBUOUI>2.3.CO;2.
- Boyle, W.A. 2008. Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. *J. Anim. Ecol.* 77(6): 1122–1128. doi:10.1111/j.1365-2656.2008.01451.x. PMID:18657208.
- Brenkman, S.J., and Corbett, S.C. 2005. Extent of anadromy in bull trout and implications for conservation of a threatened species. *N. Am. J. Fish. Manage.* 25(3): 1073–1081. doi:10.1577/M04-132.1.
- Bruggeman, J.E., White, P.J., Garrott, R.A., and Watson, F.G.R. 2008. Partial migration in Central Yellowstone bison. *In Terrestrial ecology. Edited by R.A. Garrott, P.J. White, and F.G.R. Watson. Elsevier.* pp. 217–235. doi:10.1016/S1936-7961(08)00212-1.
- Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A.J.M., Morellet, N., Kjellander, P., Linnell, J.D.C., Mysterud, A., Neteler, M., Delucchi, L., Ossi, F., and Urbano, F. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos*, 120(12): 1790–1802. doi:10.1111/j.1600-0706.2011.19441.x.
- Carlson, S.M., Rich, H.B., Jr., and Quinn, T.P. 2004. Reproductive life-span and sources of mortality for alternative male life-history strategies in sockeye salmon, *Oncorhynchus nerka*. *Can. J. Zool.* 82(12): 1878–1885. doi:10.1139/z04-189.
- Cote, D., Moulton, S., Frampton, P.C.B., Scruton, D.A., and McKinley, R.S. 2004. Habitat use and early winter movements by juvenile Atlantic cod in a coastal area of Newfoundland. *J. Fish Biol.* 64(3): 665–679. doi:10.1111/j.1095-8649.2004.00331.x.
- Engstedt, O., Stenroth, P., Larsson, P., Ljunggren, L., and Elfman, M. 2010. Assessment of natal origin of pike (*Esox lucius*) in the Baltic Sea using Sr:Ca in otoliths. *Environ. Biol. Fishes.* 89(3–4): 547–555. doi:10.1007/s10641-010-9686-x.
- Fast, D.E., Bosch, W.J., Johnston, M.V., Strom, C.R., Knudsen, C.M., Fritts, A.L., Temple, G.M., Pearsons, T.N., Larsen, D.A., Dittman, A.H., and May, D. 2015. A Synthesis of findings from an integrated hatchery program after three generations of spawning in the natural environment. *N. Am. J. Aquacult.* 77(3): 377–395. doi:10.1080/15222055.2015.1024360.
- Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Rev. Fish Biol. Fish.* 6(4): 379–416. doi:10.1007/BF00164323.
- Fleming, I.A., and Reynolds, J.D. 2004. Salmonid breeding systems. *In Evolution illuminated: salmon and their relatives. Edited by A.P. Hendry and S.C. Stearns. Oxford University Press, USA.* pp. 264–294.
- Fukumori, K., Okuda, N., Hamaoka, H., Fukumoto, T., Takahashi, D., and Omori, K. 2008. Stable isotopes reveal life history polymorphism in the coastal fish *Apogon notatus*. *Mar. Ecol. Prog. Ser.* 362: 279–289. doi:10.3354/meps07397.
- Gaidet, N., and Lecomte, P. 2013. Benefits of migration in a partially-migratory tropical ungulate. *BMC Ecol.* 13: 36. doi:10.1186/1472-6785-13-36. PMID:24079650.
- Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., and Rubin, D.B. 2013. Bayesian data analysis. 3rd ed. Chapman and Hall/CRC, Boca Raton, Fla.
- Gillanders, B.M., Izzo, C., Doubleday, Z.A., and Ye, Q. 2015. Partial migration:

- growth varies between resident and migratory fish. *Biol. Lett.* **11**(3): 20140850. doi:10.1098/rsbl.2014.0850. PMID:25788490.
- Gillis, E.A., Green, D.J., Middleton, H.A., and Morrissey, C.A. 2008. Life history correlates of alternative migratory strategies in American Dippers. *Ecology*, **89**(6): 1687–1695. doi:10.1890/07-1122.1. PMID:18589532.
- Godinho, A.L., and Kynard, B. 2006. Migration and spawning of radio-tagged zulega *Prochilodus argenteus* in a dammed Brazilian river. *Trans. Am. Fish. Soc.* **135**(3): 811–824. doi:10.1577/T04-176.1.
- Godinho, A.L., Kynard, B., and Godinho, H.P. 2007. Migration and spawning of female surubim (*Pseudoplatystoma corruscans*, Pimelodidae) in the São Francisco River, Brazil. *Environ. Biol. Fishes*, **80**(4): 421–433. doi:10.1007/s10641-006-9141-1.
- Grayson, K.L., and Wilbur, H.M. 2009. Sex- and context-dependent migration in a pond-breeding amphibian. *Ecology*, **90**(2): 306–312. doi:10.1890/08-0935.1. PMID:19323212.
- Grayson, K.L., Bailey, L.L., and Wilbur, H.M. 2011. Life history benefits of residency in a partially migrating pond-breeding amphibian. *Ecology*, **92**(6): 1236–1246. doi:10.1890/11-0133.1. PMID:21797152.
- Grist, H., Daunt, F., Wanless, S., Burthe, S.J., Newell, M.A., Harris, M.P., and Reid, J.M. 2017. Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird. *J. Anim. Ecol.* **86**(5): 1010–1021. doi:10.1111/1365-2656.12691. PMID:28502109.
- Hansen, B.B., Aanes, R., and Sæther, B.-E. 2010. Partial seasonal migration in high-arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Can. J. Zool.* **88**(12): 1202–1209. doi:10.1139/Z10-086.
- Harstad, D.L., Larsen, D.A., and Beckman, B.R. 2014. Variation in minijack rate among hatchery populations of Columbia River basin Chinook salmon. *Trans. Am. Fish. Soc.* **143**(3): 768–778. doi:10.1080/00028487.2014.886621.
- Hayward, A., and Gillooly, J.F. 2011. The cost of sex: quantifying energetic investment in gamete production by males and females. *PLoS ONE*, **6**(1): e16557. doi:10.1371/journal.pone.0016557. PMID:21283632.
- Healey, M.C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In *Pacific salmon life histories*. Edited by C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 311–394.
- Hebblewhite, M., and Merrill, E.H. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. *Oikos*, **120**(12): 1860–1870. doi:10.1111/j.1600-0706.2011.19436.x.
- Hebblewhite, M., Merrill, E., and McDermid, G. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecol. Monogr.* **78**(2): 141–166. doi:10.1890/06-1708.1.
- Hendry, A.P., and Berg, O.K. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. *Can. J. Zool.* **77**(11): 1663–1675. doi:10.1139/z99-158.
- Hendry, A.P., and Stearns, S.C. (Editors). 2004. *Evolution illuminated: salmon and their relatives*. Oxford University Press, USA.
- Hildén, O. 1982. Winter ecology and partial migration of the goldcrest *Regulus regulus* in Finland. *Ornis Fenn.* **59**(2): 99–122.
- Hutchings, J.A., and Jones, M.E. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* **55**(S1): 22–47. doi:10.1139/d98-004.
- Jahn, A.E., Levey, D.J., Hostetler, J.A., and Mamani, A.M. 2010. Determinants of partial bird migration in the Amazon Basin. *J. Anim. Ecol.* **79**(5): 983–992. doi:10.1111/j.1365-2656.2010.01713.x. PMID:20546065.
- Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. *Rev. Fish. Biol. Fish.* **3**(4): 348–365. doi:10.1007/BF00043384.
- Kerr, L.A., Secor, D.H., and Piccoli, P.M. 2009. Partial migration of fishes as exemplified by the estuarine-dependent white perch. *Fisheries*, **34**(3): 114–123. doi:10.1577/1548-8446-34.3.114.
- Kerr, L.A., Cadrin, S.X., and Secor, D.H. 2010. The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. *Ecol. Appl.* **20**(2): 497–507. doi:10.1890/08-1382.1. PMID:20405802.
- Kitamura, T., Kume, M., Takahashi, H., and Goto, A. 2006. Juvenile bimodal length distribution and sea-run migration of the lower modal group in the Pacific Ocean form of three-spined stickleback. *J. Fish Biol.* **69**(4): 1245–1250. doi:10.1111/j.1095-8649.2006.01184.x.
- Koizumi, I., Yamamoto, S., and Maekawa, K. 2006. Female-biased migration of stream-dwelling Dolly Varden in the Shiisorapuchi River, Hokkaido, Japan. *J. Fish Biol.* **68**(5): 1513–1529. doi:10.1111/j.0022-1112.2006.001038.x.
- Kokko, H. 2007. *Modelling for field biologists and other interesting people*. Cambridge University Press, Cambridge, U.K.
- Kokko, H. 2011. Directions in modelling partial migration: how adaptation can cause a population decline and why the rules of territory acquisition matter. *Oikos*, **120**(12): 1826–1837. doi:10.1111/j.1600-0706.2011.19438.x.
- Kristoffersen, K., Halvorsen, M., and Jørgensen, L. 1994. Influence of parr growth, lake morphology, and freshwater parasites on the degree of anadromy in different populations of Arctic char (*Salvelinus alpinus*) in northern Norway. *Can. J. Fish. Aquat. Sci.* **51**(6): 1229–1246. doi:10.1139/f94-123.
- L'Abée-Lund, J.H., Jonsson, B., Jensen, A.J., Sættlem, L.M., Heggberget, T.G., Johnsen, B.O., and Naesje, T.F. 1989. Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. *J. Anim. Ecol.* **58**(2): 525–542. doi:10.2307/4846.
- Lack, D. 1944. The problem of partial migration. *Br. Birds*, **37**: 122–130.
- Larsen, D.A., Beckman, B.R., and Cooper, K.A. 2010. Examining the conflict between smolting and precocious male maturation in spring (stream-type) Chinook salmon. *Trans. Am. Fish. Soc.* **139**(2): 564–578. doi:10.1577/T08-209.1.
- Larsen, D.A., Harstad, D.L., Strom, C.R., Johnston, M.V., Knudsen, C.M., Fast, D.E., Pearsons, T.N., and Beckman, B.R. 2013. Early life history variation in hatchery- and natural-origin spring Chinook salmon in the Yakima River, Washington. *Trans. Am. Fish. Soc.* **142**(2): 540–555. doi:10.1080/00028487.2012.750626.
- Lundberg, P. 1985. Dominance behaviour, body weight and fat variations, and partial migration in European blackbirds *Turdus merula*. *Behav. Ecol. Sociobiol.* **17**(2): 185–189. doi:10.1007/BF00299250.
- Lundberg, P. 2013. On the evolutionary stability of partial migration. *J. Theor. Biol.* **321**: 36–39. doi:10.1016/j.jtbi.2012.12.017. PMID:23306057.
- May, M.L. 2013. A critical overview of progress in studies of migration of dragonflies (Odonata: Anisoptera), with emphasis on North America. *J. Insect Conserv.* **17**(1): 1–15. doi:10.1007/s10841-012-9540-x.
- McFarlane, G.A., and King, J.R. 2003. Migration patterns of spiny dogfish (*Squalus acanthias*) in the North Pacific Ocean. *Fish. Bull. (Wash. D.C.)*, **101**(2): 358–367.
- McGuire, L.P., and Boyle, W.A. 2013. Altitudinal migration in bats: evidence, patterns, and drivers: bat altitudinal migration. *Biol. Rev. Camb. Philos. Soc.* **88**(4): 767–786. doi:10.1111/brv.12024. PMID:23480862.
- McMillan, J.R., Dunham, J.B., Reeves, G.H., Mills, J.S., and Jordan, C.E. 2012. Individual condition and stream temperature influence early maturation of rainbow and steelhead trout, *Oncorhynchus mykiss*. *Environ. Biol. Fishes*, **93**(3): 343–355. doi:10.1007/s10641-011-9921-0.
- Mogen, J.T., and Kaeding, L.R. 2005. Identification and characterization of migratory and nonmigratory bull trout populations in the St. Mary River drainage, Montana. *Trans. Am. Fish. Soc.* **134**(4): 841–852. doi:10.1577/T04-143.1.
- Moore, J.W., Yeakel, J.D., Peard, D., Lough, J., and Beere, M. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. *J. Anim. Ecol.* **83**(5): 1035–1046. doi:10.1111/1365-2656.12212. PMID:24673479.
- Morita, K.M.K., and Nagasawa, T.N.T. 2010. Latitudinal variation in the growth and maturation of masu salmon (*Oncorhynchus masou*) parr. *Can. J. Fish. Aquat. Sci.* **67**(6): 955–965. doi:10.1139/F10-028.
- Morita, K., Yamamoto, S., and Hoshino, N. 2000. Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming. *Can. J. Fish. Aquat. Sci.* **57**(6): 1300–1306. doi:10.1139/f00-050.
- Morita, K., Tamate, T., Kuroki, M., and Nagasawa, T. 2014. Temperature-dependent variation in alternative migratory tactics and its implications for fitness and population dynamics in a salmonid fish. *J. Anim. Ecol.* **83**(6): 1268–1278. doi:10.1111/1365-2656.12240. PMID:24773465.
- Morrison, T.A., and Bolger, D.T. 2012. Wet season range fidelity in a tropical migratory ungulate. *J. Anim. Ecol.* **81**(3): 543–552. doi:10.1111/j.1365-2656.2011.01941.x. PMID:22256947.
- Morrissey, C.A. 2004. Effect of altitudinal migration within a watershed on the reproductive success of American dippers. *Can. J. Zool.* **82**(5): 800–807. doi:10.1139/z04-042.
- Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. *J. Zool. (Lond.)*, **247**(4): 479–486. doi:10.1111/j.1469-7998.1999.tb01011.x.
- Mysterud, A., Loe, L.E., Zimmermann, B., Bischof, R., Veiberg, V., and Meisingset, E. 2011. Partial migration in expanding red deer populations at northern latitudes — a role for density dependence? *Oikos*, **120**(12): 1817–1825. doi:10.1111/j.1600-0706.2011.19439.x.
- Naidoo, R., Du Preez, P., Stuart-Hill, G., Jago, M., and Wegmann, M. 2012. Home on the range: factors explaining partial migration of African buffalo in a tropical environment. *PLoS ONE*, **7**(5): e36257. doi:10.1371/journal.pone.0036257. PMID:22570722.
- Nicholson, M.C., Bowyer, R.T., and Kie, J.G. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. *J. Mammal.* **78**(2): 483–504. doi:10.2307/1382900.
- Nordeng, H. 1983. Solution to the char problem based on Arctic char (*Salvelinus alpinus*). *Can. J. Fish. Aquat. Sci.* **40**(9): 1372–1387. doi:10.1139/f83-159.
- Ohms, H.A., Sloat, M.R., Reeves, G.H., Jordan, C.E., and Dunham, J.B. 2013. Influence of sex, migration distance, and latitude on life history expression in steelhead and rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* **71**(1): 70–80. doi:10.1139/cjfas-2013-0274.
- Pearse, D., Miller, M.R., Abadía-Cardoso, A., and Carlos Garza, J. 2014. Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in steelhead/rainbow trout. *Proc. R. Soc. B Biol. Sci.* **281**: 20140012. doi:10.1098/rspb.2014.0012.
- Perez, C., Granadeiro, J.P., Dias, M.P., Alonso, H., and Catry, P. 2014. When males are more inclined to stay at home: insights into the partial migration of a pelagic seabird provided by geolocators and isotopes. *Behav. Ecol.* **25**(2): 313–319. doi:10.1093/beheco/art119.
- Pérez-Tris, J., and Tellería, J.L. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. *J. Anim. Ecol.* **71**(2): 211–224. doi:10.1046/j.1365-2656.2002.00590.x.
- Power, G. 1980. The brook charr, *Salvelinus fontinalis*. In *Charrs, salmonid fishes of the genus Salvelinus*. Edited by E.K. Balon. Dr. W. Junk Publishers, The Hague. pp. 141–203.

- Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Bethesda, Md.
- R Core Team. 2017. R Foundation for Statistical Computing, Vienna, Austria.
- Rabenold, K.N., and Rabenold, P.P. 1985. Variation in altitudinal migration, winter segregation, and site tenacity in two subspecies of Dark-eyed Juncos in the Southern Appalachians. *Auk*, **102**(4): 805–819.
- Rikardsen, A.H., and Elliott, J.M. 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. *J. Fish Biol.* **56**(2): 328–346. doi:10.1111/j.1095-8649.2000.tb02110.x.
- Rolandson, C.M., Solberg, E.J., Saether, B.-E., Moorter, B.V., Herfindal, I., and Bjørneraas, K. 2017. On fitness and partial migration in a large herbivore — migratory moose have higher reproductive performance than residents. *Oikos*, **126**(4): 547–555. doi:10.1111/oik.02996.
- Ruzzante, D.E., Mariani, S., Bekkevoold, D., André, C., Mosegaard, H., Clausen, L.A.W., Dahlgren, T.G., Hutchinson, W.F., Hatfield, E.M.C., Torstensen, E., Brigham, J., Simmonds, E.J., Laikre, L., Larsson, L.C., Stet, R.J.M., Ryman, N., and Carvalho, G.R. 2006. Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. *Proc. R. Soc. B Biol. Sci.* **273**(1593): 1459–1464. doi:10.1098/rspb.2005.3463.
- Sahashi, G., and Morita, K. 2013. Migration costs drive convergence of threshold traits for migratory tactics. *Proc. R. Soc. B Biol. Sci.* **280**(1773): 20132539. doi:10.1098/rspb.2013.2539.
- Schaller, G.B. 1998. *Wildlife of the Tibetan Steppe*. University of Chicago Press, Chicago, Ill.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. *Nature*, **465**(7298): 609–612. doi:10.1038/nature09060. PMID:20520713.
- Secor, D.H., Rooker, J.R., Zlokovitz, E., and Zdanowicz, V.S. 2001. Identification of riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. *Mar. Ecol. Prog. Ser.* **211**: 245–253. doi:10.3354/meps211245.
- Senior, P., Butlin, R.K., and Altringham, J.D. 2005. Sex and segregation in temperate bats. *Proc. R. Soc. B Biol. Sci.* **272**(1580): 2467–2473. doi:10.1098/rspb.2005.3237.
- Silverin, B., Viebke, P.A., and Westin, J. 1989. Hormonal correlates of migration and territorial behavior in juvenile willow tits during autumn. *Gen. Comp. Endocrinol.* **75**(1): 148–156. doi:10.1016/0016-6480(89)90020-8. PMID:2767404.
- Skov, C., Brodersen, J., Nilsson, P.A., Hansson, L.-A., and Brönmark, C. 2008. Inter- and size-specific patterns of fish seasonal migration between a shallow lake and its streams. *Ecol. Freshw. Fish.* **17**(3): 406–415. doi:10.1111/j.1600-0633.2008.00291.x.
- Skov, C., Aarestrup, K., Baktoft, H., Brodersen, J., Brönmark, C., Hansson, L.-A., Nielsen, E.E., Nielsen, T., and Nilsson, P.A. 2010. Influences of environmental cues, migration history, and habitat familiarity on partial migration. *Behav. Ecol.* **21**(6): 1140–1146. doi:10.1093/beheco/arq121.
- Skov, C., Baktoft, H., Brodersen, J., Brönmark, C., Chapman, B.B., Hansson, L.-A., and Nilsson, P.A. 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. *Proc. R. Soc. B Biol. Sci.* **278**(1710): 1414–1418. doi:10.1098/rspb.2010.2035.
- Slager, B.H., and Malcolm, S.B. 2015. Evidence for partial migration in the southern monarch butterfly, *Danaus erippus*, in Bolivia and Argentina. *Biotropica*, **47**(3): 355–362. doi:10.1111/btp.12206.
- Sloat, M.R., Reeves, G.H., and Jonsson, B. 2014. Individual condition, standard metabolic rate, and rearing temperature influence steelhead and rainbow trout (*Oncorhynchus mykiss*) life histories. *Can. J. Fish. Aquat. Sci.* **71**(4): 491–501. doi:10.1139/cjfas-2013-0366.
- Smith, H.G., and Nilsson, J.-Å. 1987. Intraspecific variation in migratory pattern of a partial migrant, the Blue Tit (*Parus caeruleus*): an evaluation of different hypotheses. *Auk*, **104**(1): 109–115. doi:10.2307/4087239.
- Swingland, I.R., and Lessells, C.M. 1979. The natural regulation of giant tortoise populations on Aldabra Atoll. Movement polymorphism, reproductive success and mortality. *J. Anim. Ecol.* **48**(2): 639–654. doi:10.2307/4184.
- Takii, A., Izumiyama, S., and Taguchi, M. 2012. Partial migration and effects of climate on migratory movements of Sika Deer in Kirigamine Highland, central Japan. *Mamm. Study*, **37**(4): 331–340. doi:10.3106/041.037.0407.
- Taylor, C.M., and Norris, D.R. 2007. Predicting conditions for migration: effects of density dependence and habitat quality. *Biol. Lett.* **3**(3): 280–284. doi:10.1098/rsbl.2007.0053. PMID:17374588.
- Thompson, N.F., Leblanc, C.A., Romer, J.D., Schreck, C.B., Blouin, M.S., and Noakes, D.L.G. 2016. Sex-biased survivorship and differences in migration of wild steelhead (*Oncorhynchus mykiss*) smolts from two coastal Oregon rivers. *Ecol. Freshw. Fish.* **25**(4): 642–651. doi:10.1111/eff.12242.
- Titus, R.G., and Mosegaard, H. 1992. Fluctuating recruitment and variable life history of migratory brown trout, *Salmo trutta* L., in a small, unstable stream. *J. Fish Biol.* **41**(2): 239–255. doi:10.1111/j.1095-8649.1992.tb02654.x.
- Trivers, R.L., and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**(4068): 90–92. doi:10.1126/science.179.4068.90. PMID:4682135.
- Trotter, P.C. 1989. Coastal cutthroat trout: a life history compendium. *Trans. Am. Fish. Soc.* **118**(5): 463–473. doi:10.1577/1548-8659(1989)118<0463:CCTALH>2.3.CO;2.
- Tsukamoto, K., Nakai, I., and Tesch, W.-V. 1998. Do all freshwater eels migrate? *Nature*, **396**(6712): 635–636. doi:10.1038/25264.
- Van Deelen, T.R., Campa, H., Hamady, M., and Haufler, J.B. 1998. Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan. *J. Wildl. Manage.* **62**(1): 205–213. doi:10.2307/3802280.
- White, P.J., Davis, T.L., Barnowe-Meyer, K.K., Crabtree, R.L., and Garrott, R.A. 2007. Partial migration and philopatry of Yellowstone pronghorn. *Biol. Conserv.* **135**(4): 502–510. doi:10.1016/j.biocon.2006.10.041.
- Yackulic, C.B., Yard, M.D., Korman, J., and Haverbeke, D.R. 2014. A quantitative life history of endangered humpback chub that spawn in the Little Colorado River: variation in movement, growth, and survival. *Ecol. Evol.* **4**(7): 1006–1018. doi:10.1002/ece3.990. PMID:24772278.