

Causes for partial migration among different taxa

Tim Oortwijn

Introduction

Partial migration in a life-history context

Migration is a common life history strategy to deal with seasons and is found in many taxa (Dingle & Drake, 2007). In the northern hemisphere this means that in general, individuals migrate southwards after the breeding season and after wintering in warmer areas they migrate northwards in spring towards their breeding areas (Richardson, 1978). And this migration is repeated yearly. There are species in which only part of the population undergoes this migration, while the other part stays in the breeding areas (Shaw & Levin, 2011). This is called partial migration and can be found in many species from different classes.

Types of partial migration

Partial migration can be divided in three types (Shaw & Levin, 2011). In type A, the whole population is in the same area during the breeding season, but during the non-breeding season, part of the population migrates to another area, whereas the other part stays in the same area (Figure 1a). In type B and C this is the other way around, the whole population is at the same area during the non-breeding season and part stays there during the breeding season, while the other part migrates to another area. The difference between type B and C is that in type B both residents and migrants breed (Figure 1b), but in type C only the migrants breed (Figure 1c).

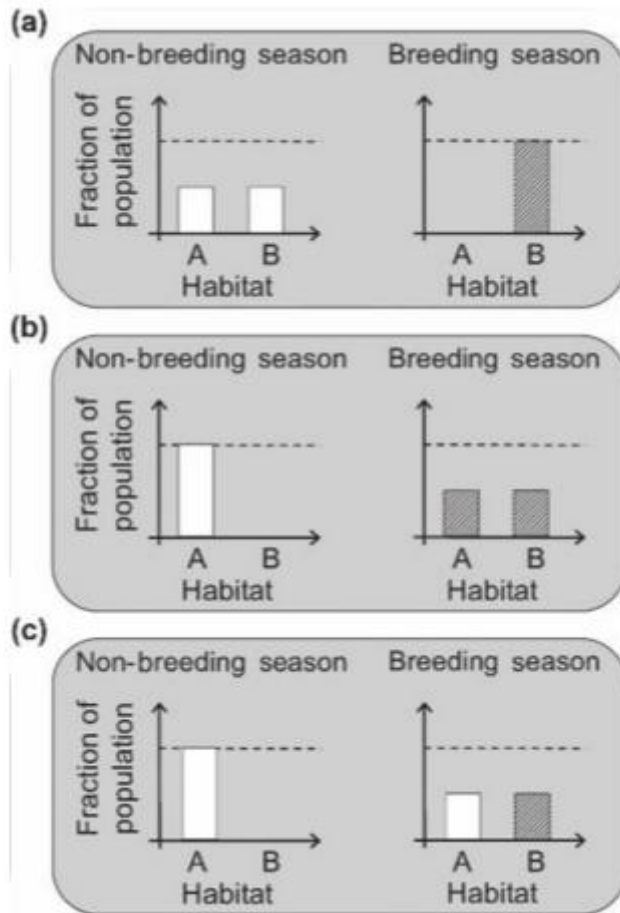


Figure 1: Schematic overview of different types of partial migration. A, residents and migrants share a breeding habitat, but spend the non-breeding season apart. B, residents and migrants share a non-breeding habitat and breed apart. C, residents and migrants are apart during the breeding season, but since migration is required for reproduction, only migrant individuals reproduce. Each panel shows the fraction of the population in each of the two habitats (A & B) during each of the two seasons. Shaded bars indicate individuals that are reproducing. Retrieved from (Shaw & Levin, 2011).

Hypotheses explaining partial migration

I found several characteristics which are potentially determining the migratory strategy of an individual: age, sex, dominance, condition and size. These determining characteristics are the basis for the six hypotheses I found in literature for the existence of partial migration. These six hypotheses can be divided in two categories; the first three are focused on survival, whereas the last three are focused on reproduction success:

1. Dominance hypothesis

This hypothesis applies to partial migration type A, with limited resources in the non-breeding season, causing migration of part of the population (Cagnacci et al., 2011; Hegemann, Marra, & Tieleman, 2015; Ketterson & Nolan, 1983; Mysterud et al., 2011). The dominant individuals which are in advantage in the competition for the limited resources stay resident, while the subdominant individuals migrate to alternative areas to avoid this competition (Cagnacci et al., 2011; Hegemann et al., 2015; Ketterson & Nolan, 1983). Therefore this is also known as the competition avoidance hypothesis (Cagnacci et al., 2011; Mysterud et al., 2011). So dominance is the main determining characteristic for individual migratory strategy in this hypothesis and that can be influenced by age, sex and size.

2. Predation avoidance hypothesis

In this hypothesis differential vulnerability for predation during the non-breeding season, causes differential migration (Skov et al., 2011), so type A partial migration. This vulnerability is size-dependent, so smaller more vulnerable individuals migrates, while bigger individuals stay resident (Skov et al., 2011).

3. Body-size hypothesis

As the name already suggests, the determining characteristic in this hypothesis is the size. Larger individuals have a lower surface to volume ratio and are therefore better able to cope with cold conditions during the non-breeding season than smaller individuals (Hegemann et al., 2015; Ketterson & Nolan, 1983). Besides they have a larger energy storage which makes them better able to survive periods of no or low food availability (Ketterson & Nolan, 1983). Larger individuals are therefore able to stay in breeding areas during the non-breeding season, but smaller individuals migrate to alternative areas (Hegemann et al., 2015; Ketterson & Nolan, 1983), type A partial migration.

4. Breeding hypothesis

This hypothesis states that only the individuals that are going to reproduce are migrating towards suitable areas for reproduction and raising young and that the other individuals stay resident (Bell et al., 1992; Chapman et al., 2012; Cryan, 2003; Engelhard & Heino, 2005; Ibáñez et al., 2009; Villa & Cockrum, 1962). This hypothesis applies to partial migration type C and the individual reproduction strategy and therefore migratory strategy can be dependent on age, sex and condition.

5. Alternative maturation hypothesis

For this hypothesis, based on a partial migration system in some fish species, no name existed yet and I call it the alternative maturation hypothesis. In this system part of the population migrates to alternative feeding habitats to grow larger than residents, which provides reproductive advantage (Jonsson & Jonsson, 1993; Kerr, Secor, & Piccoli, 2009). Residents do not take the migration risk and stay smaller. This is type A partial migration and the sex and size are determining characteristics in this hypothesis.

6. Arrival time hypothesis

Early arrival at breeding grounds is important for obtaining high quality territories, so residency is the ultimate strategy to 'arrive early' at the breeding site. The advantage of arriving early differs per sex, so the hypothesis states that the sex with the advantage stays resident and that the other sex migrates. So this is type A partial migration and the determining characteristic is sex.

Aim of this essay

In this essay I will compare the appearance of the three partial migration types among insects, mammals, fish and birds. I will also find out which of these classes support which hypotheses for partial migration. First I will analyze the classes and in the end I will make the comparison. The goal is to study whether these classes have common mechanisms for partial migration and to explore if hypotheses mentioned in one class could also be

applicable to other classes. By combining ideas about partial migration from different classes I hope to create an eye-opener for research to a certain class, which possibly creates new insights.

Insects

Insect migration

The best known example of insect migration is probably the migration of monarch butterflies *Danaus* spp., which fly from North-America to their wintering areas in Mexico every autumn with more than 100 million individuals (Wassenaar & Hobson, 1998). But also other insects migrate on a large scale, like desert locusts *Schistocerca gregaria* (Kennedy, 1951) and dragonflies *Odonata* (Russell, May, Soltesz, & Fitzpatrick, 1998). The difference between insect migration and migration of vertebrates, is that insects do not make the full round-trip migration and thus not end where they were born themselves (Holland, Wikelski, & Wilcove, 2006), but the next generations complete the cycle. Reasons for an individual insect to migrate are unclear, but it could be to enhance the circumstances in which their offspring grows up (Holland et al., 2006). While little is known about the reasons for migration among insects, partial migration is even less understood and studied. Partial migration among insects is found though, namely partial migration types A and B. Difference in migratory behavior between generations can also be seen as partial migration.

Case studies of partial migration

In two species of monarch butterflies partial migration is found (Morris, Kline, & Morris, 2015; Slager & Malcolm, 2015). In both monarchs *Danaus plexippus*, which live in North-America and southern monarchs *Danaus erripus*, which live in South-America, migratory and residential populations exist (Altizer & Davis, 2010; Slager & Malcolm, 2015). But some populations show partial migration (Morris et al., 2015; Slager & Malcolm, 2015). In both species individuals from migratory populations appeared to have larger wings than non-migrants (Altizer & Davis, 2010; Slager & Malcolm, 2015) and rearing experiments strongly indicated that wing size is genetically determined (Altizer & Davis, 2010).

In the southern monarch, individuals from the partial migratory populations migrate to higher elevations during summer and they also have larger wings than the residential butterflies which stay in the lowlands (Slager & Malcolm, 2015). But while wing size is genetically determined, possibly together with migratory behavior, migrants and residents can exchange genes during winter when both are reproductive at the same location (Slager & Malcolm, 2015). Larger winged males are better able to obtain the preferred larger winged females however (Frey, Leong, Peffer, Smidt, & Oberhauser, 1998), so the exchange could be very limited and resulting in two diverging populations both in life history strategy and in genes. Advantage of one of the strategies is unknown for this case, as well as the reason for the migration uphill.

In case of the 'North-American' monarch partially migratory populations, where residents stay in the breeding habitats during winter, while migrants winter in the south where they are reproductively inactive (Morris et al., 2015), both strategies have their benefits. Residents are able to reproduce in winter (Morris et al., 2015), without taking a risk by surviving some months before their only moment of reproduction. Hardly any butterfly survives low temperatures during winter in the breeding areas however (Morris et al., 2015)

and the mortality during migration is very low (Flockhart, Pichancourt, Norris, & Martin, 2015).

Migratory monarchs navigate both in autumn and in spring with their time-compensated sun compass (Guerra & Reppert, 2013). Besides sun, and thus light, temperature can also be a trigger to migrate in a certain direction (Guerra & Reppert, 2013). So difference in thermal and light conditions are likely to be the cause for difference in migration behavior between different generations. Why only part of a population is triggered by this is still a mystery.

My conclusion

I did not find other insect species in which partial migration is studied, but in the two discussed species I found both type A and type B partial migration. While less is known of the mechanism and the causes for partial migration in insects, it does not support any of the six hypotheses of partial migration. The differences in migratory behavior between generations in insects make this class hard to compare with the other classes, because in those classes individuals live more than one year and one individual completes the migration cycle itself.

Mammals

Mammal migration

Mammals are diverse and so are their ways of migrating. Wildebeests walk, whales swim and bats fly, for example. Contrary to insects mammals are in general long-lived animals, which reproduce more than once. To maximize their lifetime reproductive success, trade-offs between investment in survival or in offspring have to be made and migration is a possible strategy to achieve that (Cagnacci et al., 2011). Migration also is a common life-history strategy among mammals and partial migration occurs in many species too (Avgar, Street, & Fryxell, 2013), I found examples of type A and type C migration.

Case studies of partial migration

Partial migration is found in many ungulate populations (White, Davis, Barnowe-Meyer, Crabtree, & Garrott, 2007). In both roe deer *Capreolus capreolus* and red deer *Cervus elaphus*, the amount of migration is dependent on winter severity and snow depth (Cagnacci et al., 2011; Mysterud et al., 2011). The dominance hypothesis, in these studies the competition avoidance hypothesis, is mentioned as most probable cause for partial migration in these two species, in which less dominant individuals migrate to avoid competition with more dominant individuals in case of limited resources (Mysterud et al., 2011). The observation of female roe deer migrating earlier from summer habitats than the more dominant males is supporting this hypothesis (Cagnacci et al., 2011). Migration in both these species is also density dependent, with more migration at higher densities (Cagnacci et al., 2011; Mysterud et al., 2011). The opposite is found in the Yellowstone pronghorn *Antilocapra americana*, where a lower proportion of the population migrated during higher densities (White et al., 2007). Most individuals of these populations showed strong fidelity to migration patterns however, also observed in partial migratory populations of bighorn sheep *Ovis canadensis* and elks *Cervus canadensis* (White et al., 2007). Despite this some individuals also showed plasticity by changing their strategy, remarkably only from migratory to non-migratory (White et al., 2007). This supports the dominance hypothesis, because social rank in many ungulate species is found to increase with age (Côté, 2000).

Migration is found in many bat species and so is partial migration (Cryan, 2003; Ibáñez et al., 2009; Popa-Lisseanu & Voigt, 2009; Rojas-Martínez, Valiente-Banuet, Del Coro Arizmendi, Alcántara-Eguren, & Arita, 1999; Villa & Cockrum, 1962). Migratory populations of long-nosed bats, *Leptonycteris curasoae*, are only found in the northern part of their distribution area in northern America, because of seasonal limitations in terms of resources (Rojas-Martínez et al., 1999). In some other species migration is sexual segregated and only females migrate to areas with the right conditions for giving birth and raising young (Cryan, 2003; Ibáñez et al., 2009; Villa & Cockrum, 1962), so supporting the breeding hypothesis. Breeding happens in winter areas and males have no role in raising their young, so they do not need to migrate for that and apparently is not needed for their survival to also migrate to better resources.

My conclusion

I did not find studies of partial migration in other mammalian groups as well as the groups discussed, so conclusions for mammals will be drawn based on ungulates and bats. Partial migration among appeared to be different between these groups however, I found that the ungulates belong to type A partial migration, while the bats belong to type C. Ungulates support the dominance hypothesis, making less dominant individuals migrate in case of few resources. Competition avoidance is a characteristic which makes the survival of less dominant individuals higher than when they would stay and would not be able to make enough use of the limited resources. Partial migration in bats appears to be sex-biased migration. Only females migrate to give birth and raise young in the most suitable habitat and males do not need to migrate for their survival and own offspring. Bats therefore support the breeding hypothesis.

Fishes

Fish migration

Migration of fish is observed since a long time already and can be separated in different types (Hoar, 1953). Anadromous fish live as adults in the sea and migrate to freshwater for reproduction, salmon for example (Hoar, 1953). The opposite are catadromous fish which reproduce in salt water, while living as adults in freshwater, with eels as an example (Hoar, 1953). Beside that there are also species which migrate only in the ocean, oceanodromy, or only in fresh water, potamodromy (Chapman et al., 2012; Hoar, 1953).

Due to this longtime attention to migration of fish, also partial migration in fish is studied and found to be a common phenomenon (Chapman et al., 2012; Jonsson & Jonsson, 1993). When investigating the taxonomic overview of partial migratory fish created by Chapman et al. (2012), two main types of partial migration can be distinguished, namely type A and type C.

Case studies of partial migration

Many studied species are partially anadromous, which means that the residents stay in fresh water the whole year, while the migrants migrate to salt water after the breeding season (Jonsson & Jonsson, 1993; Kerr et al., 2009; Kitamura, Kume, Takahashi, & Goto, 2006; Limburg et al., 2001; Yang, Arai, Liu, & Miyazaki, 2006). In two of these studies it is not clear what determines which part of the population migrates and why (Limburg et al., 2001; Yang et al., 2006), but one system is quite well studied. It is found in many salmonid species

Salmonidae as well as in the well researched white perch *Morone americana* (Jonsson & Jonsson, 1993; Kerr et al., 2009). In this system migrants are leaving the reproduction site for an alternative feeding habitat, in which they are able to grow faster and become bigger than residents (Figure 2) (Jonsson & Jonsson, 1993; Kerr et al., 2009). Determining characteristics for individuals to migrate are size and sex (Jonsson & Jonsson, 1993; Kerr et al., 2009). Migrants have higher growth rates than residents already before migration, possibly due to local favorable conditions (Jonsson & Jonsson, 1993; Kerr et al., 2009). The bigger part of migrants are females whereas among residents there are more males, because the advantage in terms of reproductive fitness is higher for females than for males (Jonsson & Jonsson, 1993; Kerr et al., 2009). Size of females is namely a determining factor for their reproductive fitness, because large females have a higher egg production, obtain higher quality territories and are better able to defend their eggs (Jonsson & Jonsson, 1993). Larger males win competition over females and are able to defend a territory, but smaller males can use the 'sneaker strategy', in which they try to fertilize some eggs, which are used to be for a large dominant male (Jonsson & Jonsson, 1993). While migration brings costs such as higher predation risks and physiological costs (Kerr et al., 2009), the relative advantage for many males is probably not big enough to migrate.

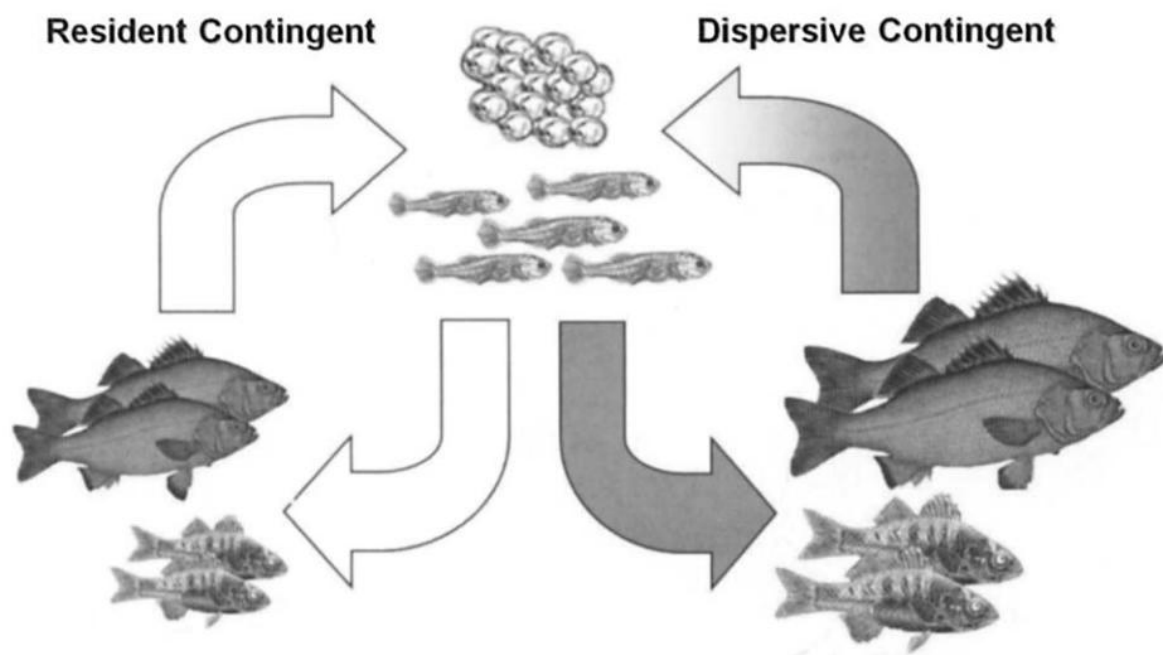


Figure 2: Life cycle of white perch, a partial migratory fish. Gray arrows represent movement into brackish water and white arrows represent movement in fresh water. From Kerr et al. (2009).

Type A partial migration is also found in the spotnape cardinalfish *Apogon notatus* and in the bream *Abramis brama*, respectively an oceanodromous and a potamodromous species (Fukumori et al., 2008; Skov et al., 2011). In the latter case, migratory behavior was found to be size dependent, with smaller individuals as migrants (Skov et al., 2011), which was also found in the three-spined stickleback *Gasterosteus aculeatus*, an anadromous species (Kitamura et al., 2006). Higher predation vulnerability among smaller individuals is mentioned as cause for this (Skov et al., 2011).

In the orange roughy *Hoplostethus atlanticus* and in the Atlantic herring *Clupea harengus*, two type C partial migratory fish species, migratory behavior was dependent on condition (Bell et al., 1992; Engelhard & Heino, 2005). Without optimal conditions individuals skipped migration and therefore also reproduction (Bell et al., 1992; Engelhard & Heino, 2005). Condition is also connected to size and therefore also age, larger fish are better swimmers and their condition is therefore earlier sufficient to migrate and reproduce than the condition of young and small fish (Engelhard & Heino, 2005).

My conclusion

As I found two different types of partial migration within fish, causes for partial migration are different also within fish. Determining characteristics for type A partial migration are size, sex or unknown. In most of these species migrants go to high quality food areas and where they are able to grow larger, providing a higher individual reproductive fitness, supporting the alternative maturation hypothesis. As females profit more from this, partial migration was also sex dependent. The cause for partial migration in this case can be individual growth rate, but apart from that every individual has to make the trade-off between migrating with risks and potentially higher fitness and staying resident without risks, but also a lower fitness potential. The predation avoidance hypothesis is another cause of partial migration for fish I found, caused by different predation vulnerability per individual size. Type C partial migration in fish is caused by differences in individual conditions, which could be influenced by size and age, because fish without a sufficient size are not migrating towards spawning grounds for reproduction, but stay resident in the non-breeding site. So I also found support for the breeding hypothesis in fish.

Birds

Bird migration

Migration of birds is world-wide known and this migration is well researched (Richardson, 1978). So is partial migration, which is also a wide-spread phenomenon among birds (Ketterson & Nolan, 1983). Only type A partial migration is found in birds though.

For this partial migration in birds three hypotheses are mentioned in general, namely the dominance hypothesis, body-size hypothesis and arrival time hypothesis (Ketterson & Nolan, 1983). Studies of different species support these different hypotheses.

Case studies of partial migration

The dominance hypothesis, states that subdominant individuals migrate because of low chances in the competition with dominant individuals for limited resources during the non-breeding season (Ketterson & Nolan, 1983). When dominance is sex-related and males are more dominant than females, this leads to higher proportion of females migrating compared to males (Adriaensen & Dhondt, 1990). Size is another dominance determining factor and the finding that residents are larger than migrants supports the dominance hypothesis (Hegemann et al., 2015).

Larger residents can also be explained by the body-size hypothesis however, because larger individuals are better able to handle cold, because of their lower surface area to volume ratio (Hegemann et al., 2015). Larger individuals are also better able to survive periods without available food sources, due to bad conditions, because of larger energy storage (Boyle, 2008). On the other hand smaller individuals have less requirements than larger

individuals and can therefore stay resident, while larger individuals have to migrate due to limited resources (Jahn, Levey, Hostetler, & Mamani, 2010).

Since early arrival at breeding sites is very important for obtaining a high quality territory, there is always a pressure to migrate earlier or faster than conspecifics (Kokko, 1999). Staying resident instead of migrating is a better strategy in terms of getting a high quality territory (Adriaensen & Dhondt, 1990; Kokko, 1999). Partial migration is often sex-biased and according to the arrival hypothesis, the sex with the most reproductive advantage of early arrival is dominant in the resident group (Kokko, 1999). This can be either males (Fudickar, Schmidt, Hau, Quetting, & Partecke, 2013) or females (Jahn et al., 2010). The reproductive advantage of residency can also be age-dependent, young males that have to get familiar with potential territories are more advantaged in staying than older males (Jahn et al., 2010).

My conclusion

Despite that I only found partial migration type A in birds, the causes for partial migration are different. Determining characteristics vary and I found age, sex, dominance and size. In general two main causes for partial migration in the three hypotheses can be distinguished, the dominance and body-size hypothesis are both related to survival during the non-breeding season with its accessory hard conditions, whereas the arrival hypothesis focuses on the advantages for the next breeding season. In short, survival and reproduction.

Discussion

Partial migration types

Among the three different partial migration types as explained in Figure 1, type A is the most common and is found in all studied classes: insects, mammals, fishes and birds (Table 1). Type B is only found in one butterfly species, but the life cycle of migratory insects differs from the other classes anyway, so it is hard to compare partial migration causes with the other classes. Type C partial migration is only found in mammals and fish. So the classes show some differences with respect to the partial migration types.

Table 1: Overview of distribution of different partial migration types and determining factors of partial migration among insects, mammals, fishes and birds. The three partial migration types can be found back in Figure 1, and the strategy determining characteristics are: A, age. B, sex. C, dominance. D, condition. E, size. F, unknown.

| Partial migration types Strategy depends on | A | | | | | | B | | | | | | C | | | | | |
|--|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | A | B | C | D | E | F | A | B | C | D | E | F |
| Insects | | | | | | X | | | | | | X | | | | | | |
| Mammals | | | X | | | | | | | | | | | X | | | | |
| Fishes | | X | | | X | X | | | | | | | | | | X | | |
| Birds | X | X | X | | X | | | | | | | | | | | | | |

Zooming in at the migration types, more differences between classes and be observed in terms of determining characteristics for the migratory behavior. I found partial migration type C in both mammals and fishes for example, but the determining characteristic in mammals is sex, while this is condition in fishes. This suggests that the underlying mechanism of partial migration differs between the classes, despite the same partial

migration type. These determining characteristics also show variation within class and partial migration type. When different characteristics are reason for migratory strategy, the underlying mechanism presumably also differs. Characteristics as dominance can be linked to all other characteristics (age, sex, condition and size) however. The listed characteristics are all able to be decisive on itself though, despite influence of other characteristics. In roe deer for example, more females are migrants compared to males because they are less dominant (Cagnacci et al., 2011), but the most dominant females are possibly less likely to migrate than less dominant males. In this case it the decisive characteristic is dominance. But in the example of the European blackbird *Turdus merula*, more females are migrants compared to males, because males have a higher reproductive advantage of being resident than females (Fudickar et al., 2013). In this species males could be more dominant than females too, but the decisive characteristic for migratory strategy here is sex and not dominance. So the type of partial migration and therefore the mechanism in both these examples seems the same, but the decisive characteristic differs and therefore also the underlying mechanism.

Hypotheses for partial migration

Different causation of partial migration within a class, makes generalization within a class hard. And therefore it is also hard to say something about general differences between classes. However, it is possible to link the hypotheses for causation of partial migration as stated in the introduction to the classes (Table 2).

Table 2: Overview of support for hypotheses for partial migration by different taxa.

| | Insects | Mammals | Fishes | Birds |
|-----------------------------------|---------|---------|--------|-------|
| Dominance hypothesis | | X | | X |
| Predation avoidance hypothesis | | | X | |
| Body-size hypothesis | | | | X |
| Breeding hypothesis | | X | X | |
| Alternative maturation hypothesis | | | X | |
| Arrival time hypothesis | | | | X |

Based on the studies I found on partial migration of insects, I did not find support of insects studies for any of the hypotheses. As mentioned before, the life cycle of migrating insects is different from the other classes, with different generations finishing one migratory cycle. That makes it hard to study partial migration within insects. Comparing characteristics of generations with different migratory behavior, could be a start.

The other classes support more than one hypothesis, indicating again a lot of variation within the classes. Some hypotheses are only supported by one class, although that is not excluding the possibility for those hypotheses to be cause for partial migration in the other classes. I will briefly discuss the support for every hypothesis below, without taking the insects into account:

1. Dominance hypothesis

I found support for this hypothesis in both mammals and birds. In fishes I did not find a study in which limiting resources are mentioned as a reason to migrate. The situation in which the resources are too limited to provide the whole population and in which dominant individuals are advantaged, causing partial migration does not seem to occur in fish populations. I can

imagine though that resources could be limiting sometimes. This might only lead to increased mortality then, instead of (partial) migration, but it seems possible to me that partial migration in fishes in some situations also could be explained by this hypothesis.

2. Predation avoidance hypothesis

I only found support for this hypothesis in fishes, where smaller fishes migrate to avoid predation, although only one study suggested this (Skov et al., 2011). I did not find support for this hypothesis in the other classes. In general, size variation in mammals and birds might be smaller than in fishes and therefore also the differential predation vulnerability. I can imagine that that could be a reason that I did not find support from those classes and that this hypothesis therefore does not apply to those classes.

3. Body-size hypothesis

I only found support for this hypothesis in birds. That I did not find support for this hypothesis in fishes could be because severe conditions are not mentioned as a migratory trigger in the literature I found. I can imagine that this hypothesis could apply to mammals too. Roe deer migration is for example dependent on winter severity (Cagnacci et al., 2011), so larger individuals would be able to stay resident due to a lower surface to volume ratio. The link between body-size and dominance possibly makes it hard to distinguish this hypothesis from the dominance hypothesis and they might both play a role in some systems.

4. Breeding hypothesis

This hypothesis is directly linked to type C partial migration. I found support for the hypothesis in both mammals and fish. I did not find support for this hypothesis in bird studies. I can imagine however that especially in birds where maturation takes longer than one year, partial migration could occur, where adults migrate and immature birds do not. I do not think this hypothesis could explain sex-biased partial migration in birds though, because pregnancy in birds is relatively short, forcing both sexes to migrate to reproduce.

5. Alternative maturation hypothesis

This hypothesis is based on a certain system in fishes (Figure 2) and does therefore not apply to the other classes.

6. Arrival time hypothesis

I only found support for this hypothesis in birds. Fishes and mammals both obtain territories during the breeding season and I can therefore imagine that arrival time in these classes could be as important as for birds and therefore be a cause for partial migration in these classes too. I did not find any support for this hypothesis from those classes though.

These different hypotheses show that there is a lot of variation in the way partial migration could arise. Plasticity in migratory strategy ratios among seasons and the ability to change strategy within individuals, suggest that partial migration is plastic phenomenon, which is dependent on changing conditions (Arai, Yang, & Miyazaki, 2006; Engelhard & Heino, 2005; Hegemann et al., 2015; Skov et al., 2010; White et al., 2007). However, some studies suggest that determination of the migratory strategy has a genetic base (Altizer & Davis, 2010; Skov et al., 2010). This could indicate that the species is evolving into two (sub)species, a resident one and a migratory one.

Conclusion

Partial migration is a phenomenon which is found in many species of insects, mammals, fishes and birds. Based on the variety of types and causes for partial migration across the different classes, I conclude that there is not one common underlying mechanism causing partial migration. Systems differ within classes and can be species-specific. Besides the systems are flexible and dependent on the environmental conditions.

Most of the discussed hypotheses are described by studies from one class and the studies supporting these hypotheses are often from the same class, for example the arrival time hypothesis which is only mentioned in bird research. I showed that some hypotheses are supported by more than one class though, the dominance hypothesis for example.

Ideas from research to species of a certain class could possibly also apply to species of other classes. In this essay I provided hypotheses of the existence of partial migration in different species from different classes and discussed to which other classes these hypotheses could apply.

References

- Adriaensen, F., & Dhondt, A. A. (1990). Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. *The Journal of Animal Ecology*, , 1077-1090.
- Altizer, S., & Davis, A. K. (2010). Populations of monarch butterflies with different migratory behaviors show divergence in wing morphology. *Evolution*, 64(4), 1018-1028.
- Arai, T., Yang, J., & Miyazaki, N. (2006). Migration flexibility between freshwater and marine habitats of the pond smelt *Hypomesus nipponensis*. *Journal of Fish Biology*, 68(5), 1388-1398.
- Avgar, T., Street, G., & Fryxell, J. (2013). On the adaptive benefits of mammal migration. *Canadian Journal of Zoology*, 92(6), 481-490.
- Bell, J., Lyle, J., Bulman, C., Graham, K., Newton, G., & Smith, D. (1992). Spatial variation in reproduction, and occurrence of non-reproductive adults, in orange roughy,

Hoplostethus atlanticus Collett (*Trachichthyidae*), from south-eastern australia. *Journal of Fish Biology*, 40(1), 107-122.

Boyle, W. A. (2008). Partial migration in birds: Tests of three hypotheses in a tropical lekking frugivore. *Journal of Animal Ecology*, 77(6), 1122-1128.

Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A., Morellet, N., Neteler, M.

(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.

Chapman, B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P. A., Hansson, L., & Brönmark, C.

(2012). Partial migration in fishes: Definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*, 81(2), 479-499.

Côté, S. D. (2000). Dominance hierarchies in female mountain goats: Stability, aggressiveness and determinants of rank. *Behaviour*, 137(11), 1541-1566.

Cryan, P. M. (2003). Seasonal distribution of migratory tree bats (*Lasiurus* and *Lasionycteris*) in North America. *Journal of Mammalogy*, 84(2), 579-593.

Dingle, H., & Drake, V. A. (2007). What is migration? *Bioscience*, 57(2), 113-121.

Engelhard, G. H., & Heino, M. (2005). Scale analysis suggests frequent skipping of the second reproductive season in Atlantic herring. *Biology Letters*, 1(2), 172-175.

Flockhart, D. T. T., Pichancourt, J., Norris, D. R., & Martin, T. G. (2015). Unravelling the annual cycle in a migratory animal: Breeding-season habitat loss drives population declines of monarch butterflies. *Journal of Animal Ecology*, 84(1), 155-165.

- Frey, D., Leong, K. L., Peffer, E., Smidt, R. K., & Oberhauser, K. (1998). Mate pairing patterns of monarch butterflies (*Danaus plexippus* L.) at a California overwintering site. *Journal - Lepidopterists Society*, 52, 84-97.
- Fudickar, A. M., Schmidt, A., Hau, M., Quetting, M., & Partecke, J. (2013). Female-biased obligate strategies in a partially migratory population. *Journal of Animal Ecology*, 82(4), 863-871.
- Fukumori, K., Okuda, N., Hamaoka, H., Fukumoto, T., Takahashi, D., & Omori, K. (2008). Stable isotopes reveal life history polymorphism in the coastal fish *Apogon notatus*. *Marine Ecology Progress Series*, 362, 279-289.
- Guerra, P. A., & Reppert, S. M. (2013). Coldness triggers northward flight in remigrant monarch butterflies. *Current Biology*, 23(5), 419-423.
- Hegemann, A., Marra, P. P., & Tieleman, B. I. (2015). Causes and consequences of partial migration in a passerine bird. *The American Naturalist*, 186(4), 531-546.
- Hoar, W. S. (1953). Control and timing of fish migration. *Biological Reviews*, 28(4), 437-452.
- Holland, R. A., Wikelski, M., & Wilcove, D. S. (2006). How and why do insects migrate? *Science*, 313(5788), 794-796.
- Ibáñez, C., Guillén, A., Agirre-Mendi, P. T., Juste, J., Schreur, G., Cordero, A. I., & Popa-Lisseanu, A. G. (2009). Sexual segregation in iberian noctule bats. *Journal of Mammalogy*, 90(1), 235-243.

- Jahn, A. E., Levey, D. J., Hostetler, J. A., & Mamani, A. M. (2010). Determinants of partial bird migration in the Amazon basin. *Journal of Animal Ecology*, 79(5), 983-992.
- Jonsson, B., & Jonsson, N. (1993). Partial migration: Niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, 3(4), 348-365.
- Kennedy, J. S. (1951). The migration of the desert locust (*Schistocerca gregaria* forsk.). I. the behaviour of swarms. II. A theory of long-range migrations. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 235(625), 163-290.
- Kerr, L. A., Secor, D. H., & Piccoli, P. M. (2009). Partial migration of fishes as exemplified by the estuarine-dependent white perch. *Fisheries*, 34(3), 114-123.
- Ketterson, E. D., & Nolan Jr, V. (1983). The evolution of differential bird migration. *Current ornithology* (pp. 357-402) Springer.
- Kitamura, T., Kume, M., Takahashi, H., & 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. *Journal of Fish Biology*, 69(4), 1245-1250.
- Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, 68(5), 940-950.
- Limburg, K., Blackburn, I., Schmidt, R., Lake, T., Hasse, J., Elfman, M., & Kristiansson, P. (2001). Otolith microchemistry indicates unexpected patterns of residency and anadromy in blueback herring, *Alosa aestivalis*, in the hudson and mohawk rivers. *Bulletin Français De La Pêche Et De La Pisciculture*, (362-363), 931-938.

- Morris, G. M., Kline, C., & Morris, S. M. (2015). Status of *Danaus plexippus* population in arizona. *The Journal of the Lepidopterists' Society*, 69(2), 91-107.
- Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V., & 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.1600-0706.2010.19439.x
- Popa-Lisseanu, A. G., & Voigt, C. C. (2009). Bats on the move. *Journal of Mammalogy*, 90(6), 1283-1289.
- Richardson, W. J. (1978). Timing and amount of bird migration in relation to weather: A review. *Oikos*, , 224-272.
- Rojas-Martínez, A., Valiente-Banuet, A., Del Coro Arizmendi, M., Alcántara-Eguren, A., & Arita, H. T. (1999). Seasonal distribution of the long-nosed bat (*leptonycteris curasoae*) in north america: Does a generalized migration pattern really exist? *Journal of Biogeography*, 26(5), 1065-1077.
- Russell, R. W., May, M. L., Soltesz, K. L., & Fitzpatrick, J. W. (1998). Massive swarm migrations of dragonflies (*Odonata*) in eastern north america. *The American Midland Naturalist*, 140(2), 325-342.
- Shaw, A. K., & Levin, S. A. (2011). To breed or not to breed: A model of partial migration. *Oikos*, 120(12), 1871-1879.
- Skov, C., Aarestrup, K., Baktoft, H., Brodersen, J., Brönmark, C., Hansson, L., . . . Nilsson, P. A. (2010). Influences of environmental cues, migration history, and habitat familiarity on partial migration. *Behavioral Ecology*, , arq121.

Skov, C., Baktoft, H., Brodersen, J., Bronmark, C., Chapman, B. B., Hansson, L. A., & Nilsson, P.

A. (2011). Sizing up your enemy: Individual predation vulnerability predicts migratory probability. *Proceedings Biological Sciences*, 278(1710), 1414-1418.

Slager, B. H., & Malcolm, S. B. (2015). Evidence for partial migration in the southern monarch butterfly, *Danaus erippus*, in Bolivia and Argentina. *Biotropica*, 47(3), 355-362.

Villa, B. R., & Cockrum, E. L. (1962). Migration in the guano bat *Tadarida brasiliensis mexicana* (Saussure). *Journal of Mammalogy*, 43(1), 43-64.

Wassenaar, L., & Hobson, K. (1998). Natal origins of migratory monarch butterflies at wintering colonies in Mexico: New isotopic evidence. *Proceedings of the National Academy of Sciences of the United States of America*, 95(26), 15436-15439.

doi:10.1073/pnas.95.26.15436

White, P., Davis, T. L., Barnowe-Meyer, K. K., Crabtree, R. L., & Garrott, R. A. (2007). Partial migration and philopatry of yellowstone pronghorn. *Biological Conservation*, 135(4), 502-510.

Yang, J., Arai, T., Liu, H., & Miyazaki, N. (2006). Environmental signature in the otolith elemental fingerprint of the tapertail anchovy, *Coilia mystus*, from the Changjiang estuary, China. *Journal of Applied Ichthyology*, 22(5), 459-462.