

Chapter 12. Dispersal, Navigation, and Migration

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Dispersal, Navigation and Migration

Dispersal results in a tendency for animals that were once aggregated, to become more widely distributed through movement away from aggregations. Dispersal is often one of the first events of independent life. **Navigation** occurs in an animal's movement around their routine territory or home range, such as during daily foraging or seasonal mating. Migration is an event closely coupled to reproduction. **Migration** is the seasonal movement between a breeding site and non-breeding site. In this chapter I will consider all of these kinds of movements, but I will start with the most difficult to understand of these three processes -- dispersal.

Dispersal

Dispersal, the movement from natal site to the first breeding site or between successive breeding sites, is one of the most important life history traits. However, the genetic components of dispersal remain poorly understood (Clobert et al. 2004). There are several reasons why the evolution of dispersal remains enigmatic. First, there is confusion between definitions of **dispersal** and **migration** (above). Migration is a seasonal or recurrent movement, which is typically not associated with a change in reproductive location. Second, the confusion is exacerbated by use of the term migration rather than dispersal in the population genetic literature. While the distinction between migration and dispersal is not clear-cut in all cases (e.g., nomadic species, Dingle 1996), it has however made the study of the genetic basis of dispersal difficult.

While migration seems to be under more direct genetic control than dispersal (discussed below), dispersal seems to be more phenotypically plastic (Ims and Hjermann 2001). This does not imply that dispersal is not under genetic control, rather that its control is not simple. There are theoretical reasons to think that dispersal is a complex phenomenon (Clobert et al. 2001). First, it is increasingly recognized that dispersal has a multi-cause origin (Perrin and Goudet 2001, Gandon and Michalakis 2001, and, for examples, MacKay and Wellington 1977,

Massot and Clobert 2000, Massot et al. 2002). Second, dispersal is often condition-dependent (Ims and Hjermann 2001, Ronce et al. 2001), and potentially affected by maternal as well as environmental effects. Under such conditions, dispersal may evolve in connection with suites of traits to constitute behavioral and physiological syndromes (Dufty et al. 2002). The identification of these behavioral syndromes is of prime importance to the study of dispersal and the elucidation of behavior.

The most common aggregations found in nature are associated with the nest site. A juvenile or fledgling leaves a dense nesting site, and attempts to settle on a territory where they might live, perhaps for the rest of their life. Such long distance movement can be extreme in the case of birds. Rare dispersal records based on banding at the nest and recovery by other ornithologists have registered dispersal distances measured in 1000's of kilometers. Now this is not surprising given the flight capabilities of birds. Dispersal of mammals is measured on the scale of tens of meters and kilometers. Records for lizards place the upper limit on dispersal at 1.5 km. (Sinervo et al. 2006b). Given the length of a hatchling (2.5 cm), and the distance traveled, $1.5 \text{ km} \times 1000 \text{ m/km} \times 100 \text{ cm/m}$ this would amount to 60,000 body lengths or put into human body lengths (2m tall), the human equivalent of 120 km traveled in the first week or two of life (roughly the equivalent of 3 marathons!).

What could be worth traveling such inordinate distances?

There must at the very least be incredible energetic costs associated with such long distance moves. In addition, there may be disadvantages measured in terms of survival. Movement may elevate risk of predation. Settlement in a new area and breeding with potentially divergent genomes represents a cost of moving too far. On the other hand, mating with kin can generate a cost of inbreeding. We will explore 3 theories that might explain why and where juveniles disperse and settle:

1. inbreeding depression *versus* outbreeding depression
2. the costs of kin competition
3. colonization of new habitat.

Inbreeding Avoidance

The Fitness Consequences of Inbreeding

Inbreeding can be defined in many ways, but we generally think in terms of a simple genetic definition (Chapter 4), which has to do with mating among related individuals. However, all humans ultimately share some related individuals (e.g., the proverbial Y-chromosome Adam and mitochondrial Eve, Chapter 20) at some point during their remote past. Thus, this definition is not all that precise. A more precise definition that also has practical merit is to express **inbreeding** as the probability of the two alleles on complementary chromosomes being identical by descent. If these two copies of the allele (one from mother and one from father) are **identical by descent (IBD)**, then they must have arisen in the not-so-remote past from a single strand of DNA. Calculations concerning the probability of identity by descent has practical merit because it can be used to calculate risk that deleterious recessive mutation might show up in an inbred individual, given pedigree data. If an individual has 2 copies of a **deleterious recessive mutation**, that individual will express a trait that reduces fitness, or in the worst case of a **deleterious recessive lethal**, will cause death.

The easiest way to get two genes together that are identical by descent is from **consanguineous** mating, a mating among close kin. Consider progeny fertilized from a mating between a mother and son and try to track the alleles coming from the mother. We will track one allele, **bb**, from mother to son and from the mating of mother and son, which we will call an Oedipal mating. (Recall that each pair of chromosomes possesses 2 sister chromatids). The allele **b** is located on one of the mother's two chromosome pairs.

The son may receive one copy of allele **b** with probability of $1/2$ and the red line denotes this transmission.

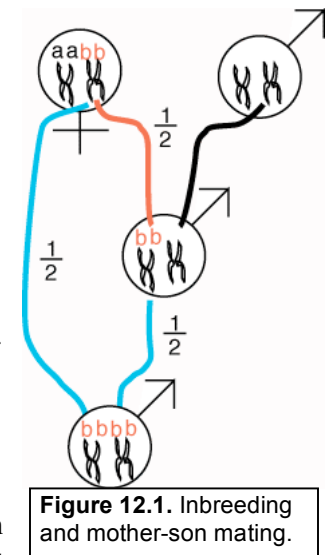


Figure 12.1. Inbreeding and mother-son mating.

The blue lines denote the 1/2 probability that the mother will contribute the same *b* allele to a progeny sired by her son that also contributes allele *b* with probability 1/2 via the second blue line.

Because all events are mutually independent, we multiply all of the probabilities to get the net probability that a child produced by an Oedipal mating possesses two *bb* alleles:

$$1/2 \times 1/2 \times 1/2 = 1/8 \quad \text{Eqn 12.1}$$

Note that the *a* allele could just as easily been transmitted to the son in the first place so the total probability that alleles in the oedipal child are identical by descent can be achieved two ways, either with allele *a* or with allele *b*. The probability of inbreeding from an Oedipal mating is:

$$2 \times 1/2 \times 1/2 \times 1/2 = 1/4 \quad \text{Eqn 12.2.}$$

Of course, there is a 3/4 probability that the Oedipal child does not carry alleles that are identical by descent at this particular locus. In this computation, we ignored inbreeding from prior generations, but *a* and *b* alleles may already be IBD. Let us consider a few simple cases to assess fitness consequences of IBD. If mom was a carrier for one deleterious recessive allele, *b*, then the probability that progeny produced from an oedipal mating would die is given by the probability that one allele is IBD = 1/8. Mom has one good copy in the form of allele *a*.

If the mom happened to carry an allele that was deleterious on each of 2 different genetic loci, we would multiply this value by 2 to get the probability of a progeny from an oedipal mating getting at least one such double whammy = $2 \times 1/8 = 1/4$. Because each individual may possess several deleterious recessive alleles, mating among related individuals typically produces **inbreeding depression** or a reduction in fitness that arises from alleles IBD. Such alleles do not have to be **lethal**; rather the combination of several **mildly deleterious alleles** can have a dramatic impact on fitness. It is thought that each human carries a few of such deleterious recessive alleles across the 30,000 or so genes in the genome. There is of course a small possibility that someone does not

carry such alleles. However, the number of these individuals, out of the 6.5 billion humans on the planet, is estimated to be around 4 to 6.

As a second example, let us consider the possibility of a sib-sib mating. We now have to keep track of the father's alleles because a grandchild can become inbred from one of the mom's alleles or one of the father's alleles. Again, we will track one allele, *bb*, from mother to son and from the mother to daughter. At the end we will then multiply the probability of a single allele being identical by descent by four (all possible alleles that might be identical by descent) to determine the overall probability that any allele is IBD.

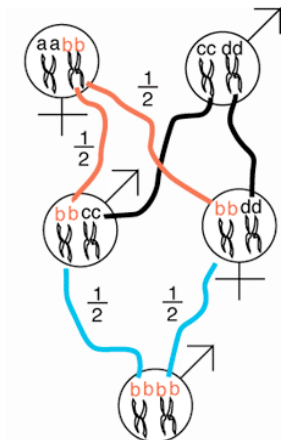


Figure 12.2. Inbreeding in brother-sister mating.

The mother gives the *b* allele to her son with probability of 1/2 and likewise the daughter receives the *b* allele with probability of 1/2 (both denoted by the red lines). Given that the daughter received the *b* allele, the daughter passes the allele on to her own progeny with probability 1/2 (blue line). Likewise, given that the son has the *b* allele he passes it on to his progeny with probability of 1/2.

The probability that a grandchild received 2 copies of allele *b* is:

$$1/2 \times 1/2 \times 1/2 \times 1/2 = 1/16 \quad \text{Eqn 12.3.}$$

The grandchild could have received *a*, *b*, *c*, or *d* alleles with the same probabilities so the probability of any two alleles at a single locus in the same individual being identical by descent is given by:

$$4 \times 1/2 \times 1/2 \times 1/2 \times 1/2 = 1/4 \quad \text{Eqn 12.4.}$$

The same logic can be used to compute the probability of two cousins yielding a child that has genes identical by descent, though the length of the paths are a little bit longer. Indeed, the logic used above can be used

to compute the **probability of inbreeding** or **identity by descent** for any **consanguineous mating**. The inbreeding in any set of pedigrees can be computed from similar **path diagrams** that chart the **genealogical relationships** among individuals. Software is available for these computations given that the complexity of calculations increases enormously for even simple pedigrees consisting of dozens of individuals.

Sex-biased Dispersal, Kin Avoidance and Kin Selection

The fitness costs arising from such inbreeding mechanisms have led various authors to propose that patterns of sex-biased dispersal are a **kin avoidance mechanism**. The tendency for offspring to breed in their natal home range is referred to as **philopatry**. Because dispersal *per se* entails costs, both sexes of progeny need not disperse to dramatically lower the probability of inbreeding. If either the female progeny disperses or the male progeny disperses, the risk of inbreeding is lowered dramatically because one of the most pernicious sources of high inbreeding (sib-sib is eliminated). In this case, we still have to worry about father-daughter or mother-son, depending on which sex dispersed). Most mammals have male-biased offspring dispersal, and the female progeny tend to be philopatric. For example, Kay Holekamp (1984) has found that female ground squirrels tend to remain near their natal nest and males disperse several hundred meters away.

The tendency for dispersal of strictly one sex cannot be explained in terms of kin avoidance. Ideas of **kin selection** (Chapter 4) are required to explain why females rather than males, for example, are the philopatric sex. If females get assistance from mothers, sisters or aunts, then they would be likely to be philopatric because of kin cooperation.

Kin selection appears to be related to levels of philopatry in other mammals and the dispersing sex is the sex least likely to benefit from kin selection. In ground squirrels females are likewise philopatric because females participate in warning calls at the colony (Holekamp and Sherman 1989).

The sex differences in dispersal can of course be reversed. For example, in cheetahs, if a female cheetah produces two or more sons, sons will form a group and cooperatively defend a territory. The brothers will even participate in cooperative breeding. It takes a few male cheetah to adequately defend a territory against other males.

Conversely a solitary male lion usually heads a pride and there is no advantage to for male philopatry in lions. Male lions disperse, whereas females remain with the pride. To further avoid inbreeding between a father and his daughters, many male lions disperse and attempt to take over another pride of lions when his daughters begin maturing. This is fairly common in other groups where the possibility of father-daughter mating arises. Recall that female lions obtain a kin benefit from protecting progeny in a crèche and from group hunting (Chapter 7).

What evidence is there that inbreeding can be costly in nature?

Very little evidence is available that directly links inbreeding depression to lack of dispersal in wild populations. Packer (1979) reported anecdotal information on a male baboon that failed to disperse at sexual maturity. He produced low surviving progeny compared to outbred males in the baboon troop.

Information on inbreeding depression *per se* is available for cases in which researchers have drawn up **pedigrees** of the sort shown in Chapter 2, but on a large scale. An elegant study of such pedigrees for sparrows on Mandarte Island (Smith 1987) illustrates real costs to inbreeding. However, in the case of the song sparrows, the effects of reduced survival in inbred individuals were most strongly manifest during periods of environmental stress. Those individuals with a higher inbreeding coefficient (e.g., the product of one or more consanguineous mating based on the pedigree computations) were more likely to die during a famine than individuals with a low inbreeding coefficient. A new study on greater reed warblers (Hansson et al. 2004), which I discuss below, suggests that philopatry may indeed exert costs of inbreeding that are actually balanced against the costs of outbreeding.

The Costs of Kin Competition

A key step in analyzing adaptive value of dispersal is identifying the selective causes underlying movement. In this regard, kin interactions (Hamilton and May 1977, Ronce et al. 1998, Perrin and Goudet 2001) appear to be one of the dominant forces in the evolution of dispersal. In birds, kin-helping behavior is linked to philopatry versus dispersal (Komdeur et al. 1997). In lizards, mother-offspring competition appears to govern dispersal (Ronce et al. 1998, Léna et al. 1998, Le Gaillard et al. 2003). In fact, kin interactions are possibly the easiest piece of information for parents to predict. Parents can manipulate offspring dispersal in many ways and also confer an advantage to philopatric or dispersing offspring (Murren et al. 2001, Léna et al. 1998). However, studying parental affects is particularly difficult because parental strategy as well as progeny fate should both be measured. This may be most readily achieved in species with alternative strategies that have genetic strategies of space use and defense (Zamudio and Sinervo 2000, Calsbeek et al. 2002; Sinervo and Clobert 2003).

We (Sinervo et al. 2006) compared survival and dispersal of *Uta stansburiana*, the side blotched lizard, on sibship-intact and randomized plots. Thus, hatchlings were released in the context of kin or were randomized away from kin. The recruitment of progeny was assessed at maturity. For the past 18 years, we have censused the adjacent meta-populations in each of the cardinal directions from the focal population where progeny have been released with the same intensity as our focal population (Fig 12.3). Dispersal of progeny between meta-populations separated by more than 200 m is rare ($P < 0.029$ have been recorded in this study). All records of long-distance dispersal events (e.g., between meta-populations), which we have detected, have occurred between our focal population and a ring of meta-populations immediately to the outside of the focal population (from 500 m – 2 km distant).

On sibship-randomized plots, we recovered 58 males at maturity out of 424 neonates, which is a survival rate of 14.8%. On sibship-intact plots, we recovered 58 males at maturity out of 910 neonates, which is a

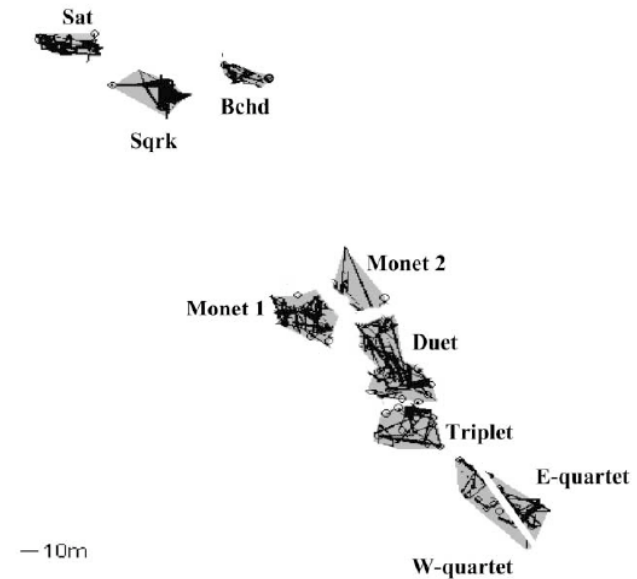


Figure 12.3. Map of one metapopulation of lizards and nine neighborhoods at our main study site at Los Banos. Neighborhoods that have been studied for 20 years are shaded. White area represents areas of unsuitable lizard habitat (e.g., grassland) or physical barriers that inhibit lizard dispersal. For instance, the two neighborhoods Equartet and W-quartet are physically close but are separated by a ridge of rocks (indicated in white) that inhibits extensive dispersal. Shown in the figure are some adult lizards that were observed only once (circles) and examples of all adult lizard movement within neighborhoods (dark lines) from the 1998 breeding season. The other populations that we study are located 500-1.5 km away at the edges of a large basin. Use google earth (coords: XXXX) to find the main study site. The other rock piles located at distance are obvious from the satellite maps. (Svensson and Sinervo 2004).

survival rate of 6.6%. Survival was doubled on sib-randomized than sib-intact plots. Higher mortality on sibship-intact plots suggests that hatchling kin competition favors dispersal not philopatry. This is because of a very simple reason. If you share genes with kin, you share many behavioral predilections that intensify the effects of density competition. Density regulation due to hatching in the same spot intensifies the mortality on kin. The levels of mortality due to kin competition are phenomenal in the side-blotched lizard.

Dispersal is often linked to trade-offs of inbreeding avoidance (e.g., deleterious recessive lethals) vs. outbreeding avoidance (e.g., mismatch of coadapted gene complexes). However, dispersal decisions in *Uta* appear to be invoked by intense kin competition. This also explains why *Uta* lizards use greenbeard recognition to cooperate (Chap 3).

The genetics and maternal influences on dispersal

In species with a clear association between genetically based morphological traits and dispersal, adaptive value of dispersal can be studied in connection with other life history traits. For example, cat coat color markers, in particular the orange allele in male cats is linked to body condition, aggressiveness and spatial movement (Pontier et al. 1995) suggesting both a genetic basis and genetic covariance between dispersal and life history traits. However, pure maternal effects could cause these associations, such that a measure of sire influence on offspring strategy would be necessary to ascertain the genetic influence on dispersal and the associated traits. Given the possibility of maternal effects on dispersal, maternal genotype is always confounded with maternal-effects plasticity. Thus, to ascertain the genetic basis of dispersal it is necessary to study effects of sire genotype *per se*.

Accumulating evidence suggests that in addition to species with a well-differentiated dispersing morph (most often found in plants and insects, but see the mole rat O’Riain et al. 1996), many species still show variation in life history traits of dispersing *versus* philopatric individuals (Bélíchon et al. 1996, Murren et al. 2001). Most reported cases treat life history traits such as survival or fecundity. However, the role of maternal investment in dispersing *versus* philopatric offspring remains to be demonstrated. Reported differences in morphology, physiology or condition between dispersive and philopatric individuals at birth are rare and sometimes contradictory (Bélíchon et al 1996, Murren et al. 2001). These contradictory results might be better understood when the causes of dispersal are considered.

For example, in the common lizard, *Lacerta vivipara*, parent-offspring competition seems to drive dispersal (Ronce et al. 1998, Le Gaillard et al. 2003). Dispersing offspring have been shown to be in better

condition compared with philopatric offspring, when dispersal was induced by the presence of a surviving mother (e.g., a high likelihood of parent-offspring interaction; Léna et al. 1998, Meylan et al. 2004). Such a result is biologically intuitive in cases where intensity of kin selection renders dispersal beneficial, even if fitness of the disperser is reduced. In the case of a mother influencing dispersal of progeny, the female parent is resolving parent-offspring conflict. The net gains of the mother surviving and inducing dispersal in her progeny, outweigh survival costs of dispersal for the progeny. In this situation, any reduction of this cost is likely to be under strong selection (Murren et al. 2001). In the common lizard, females are likely to survive across multiple episodes so the intensity of kin competition between parents and offspring are more likely to structure the patterns of dispersal, compared to the annual side-blotched lizard, *Uta stansburiana*. In *Uta* most males and females die before the eggs hatch so hatchling kin competition is more intense.

Three dispersal strategies exist in the common lizard (Cote and Clobert 2006): one type of juvenile disperses to empty habitats, another type to low density habitats, and a third type to densely populated habitats. All types display marked differences in social behavior ranking from asociality to cooperation and from neophobia to neophily. Most of the behavioral characteristics appear to be under maternal influence, although a direct genetic control cannot be excluded in some cases.

In *Uta*, three dispersal strategies are likewise present and these strategies have been linked directly to a major gene, referred to as the OBY locus

(*o*, *b*, *y* alleles), named for the alternative colors expressed on the throats of males and females (Sinervo et al. 2006ab; Sinervo and Clobert 2003) (see Chapter 4). Disperse to high density habitat is associated with *o* alleles, which induces aggression in the adult phase (Calsbeek and Sinervo 2002ab) owing to high testosterone in adult males (Sinervo et al. 2000a). Philopatric behavior is associated with *y* alleles, which

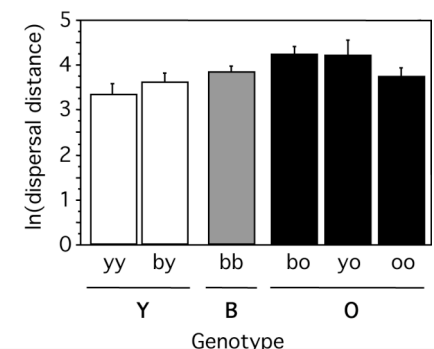


Figure 12.4. Log-transformed dispersal distance in *Uta* (Sinervo et al. 2006).

is also associated with cryptic morphology and behavior in juveniles, and female mimicry in adult males. Disperse and settle beside genetically similar individual is associated with *b* alleles. The *b* allele is also associated a cooperative greenbeard used in territory defense (Chapter 4). In *Uta*, dispersal strategies are genetic because they are associated with sire alleles in both lab crosses with field release of progeny, and in an extensive field pedigree (Figure 12.4).

However, female egg-size strategies (Sinervo et al. 2000b) also interact synergistically to enhance dispersal of *o* and *y* progeny. Using a technique of experimental gigantization of eggs and miniaturization (see Chapter 3) we were able to show that if females produced progeny carrying an orange allele (from the sire) the progeny dispersed further if the egg size of the progeny was experimentally increased. Conversely, if progeny were carrying a yellow allele (from the sire) the progeny tended to be even more philopatric. Thus, the egg size strategy of the mother can interact with dispersal genes from the sire to enhance each strategy. Notice that the tendency of progeny receiving blue alleles from the sire was not affected by the gigantization procedure, which makes sense in that settlement of blue males is contingent on finding a genetically similar partner (see Chapter 4, greenbeard settlement).

The experiments on side-blotched lizards confirm a genetic control over dispersal due to the effect of sire OBY alleles. Moreover, this genetic predilection is also modulated by maternal influences, such as egg size. In addition, maternal hormones appear to influence dispersal in lizards (reviewed in Dufty *et al.* 2004, see Chapter 16).

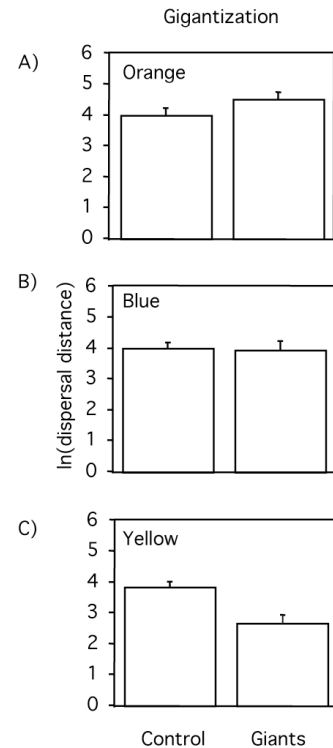


Figure 12.5. Effect of giant eggs and control eggs on dispersal of each genotype of *Uta* (based on alleles from the sire). Sinervo et al. 2006

Outbreeding depression versus inbreeding depression

While consanguineous mating generally result in inbreeding depression, it does not follow that an animal should find a mate that has a completely different genetic background. **Outbreeding depression** is the tendency to show reduced fitness in progeny that are the product of two very different genetic backgrounds. There may be an optimum level of outbreeding. Indeed the optimal dispersal distance may reflect such outbreeding depression. Go too far and you end up in the company of very different genetic mates. Outbreeding depression is thought to arise from [epistatic interactions](#) among loci similar to the effects observed when species are hybridized. Even minor incompatibility among a set of genes involved in an enzyme cascade may reduce fitness (Chapter 5).

Female Choice for Natal Song: patterns from different species

Outbreeding depression may give rise to a **behavioral block to breeding** that is analogous to species recognition mechanisms. For example, many birds are only sexually responsive to mates from their own **natal areas**. The following experiment illustrates that female birds learn songs of appropriate mates in their youth and then discriminate males that sing the right song. Recall the example of deme recognition in the Chapter 5 on speciation. Baker (1981) used tutor males to teach young female birds a song dialect. Songs similar to the tutor songs were presented to the females and songs from a different area were presented to the females when they reached maturity.

Baker (1981) found that female white-crowned sparrows responded positively to male courtship songs at a higher rate if the song was derived from their home dialect compared to an alien dialect. This kind of dialect recognition may be generic to songbird discrimination systems. Moreover, examples of **reinforcement speciation** (e.g., see the ring species of Phylloscopine warblers, or flycatchers, Chap. 5) indicate that among bird species, outbreeding often generates hybrid unfitness.

However, demonstrating a more subtle depression in fitness due to inbreeding *versus* outbreeding among races of birds or indeed any other animal is challenging. Two recent studies specifically address this issue.

For many years, the only example of outbreeding depression was a demonstration by Waser and Price (1981), who showed that outcrossing plants from further than 50 m generated depressed fitness compared to crosses of adjacent plants or crosses between plants located 10 m away.

The first animal study to address the potential effects of long versus short distance dispersal (within *versus* between demes), *versus* philopatry, has only recently been conducted, by a research group at Lund University in the south of Sweden (Hansson et al. 2004).

Hansson et al. (2004) used capture-recapture studies in combination with multilocus microsatellite genotypes to score greater reed warblers, *Acrocephalus arundinaceus*, at a Swedish study site as philopatric individuals or short- *versus* long-distance dispersing immigrants. The long distance and short distance dispersers had a significantly different multilocus microsatellite genetic profile. In particular, they used the presence of novel alleles; alleles that were never observed in pedigree of philopatric individuals for the focal population (11 year pedigree). The novel allele technique makes use of the fact that immigration has continuously brought in novel alleles to the population. Hansson et al. (2004) created three categories of birds in the cohorts of 1987–1996:

1. philopatric individuals ($n = 64$ males, 65 females),
2. immigrants without novel alleles (i.e., short-distance dispersers; $n = 56$ males, 64 females),
3. novel-allele immigrants (i.e., long-distance dispersers; $n = 21$ males, 29 females).

They then performed comparisons of lifetime reproductive success (LRS) and survival rates of these three dispersal categories. Their results indicated that short- and long-distance dispersers were of poor phenotypic quality. Of course, one of the obvious explanations for the low phenotypic quality is that the immigrant males attracted few females because they were poorly adapted to the local *social environment* and sang songs that females found unattractive. They did not specifically collect this data on mate choice, however, such effects are likely given a recent study on a 2nd avian model system, the song sparrow (see below).

In females, the number of local recruits, correcting for number of breeding years, differed between dispersal categories in a pattern that suggests an intermediate optimum for the dispersal distance. Among males, immigrants categorized as long-distance dispersers had the lowest LRS and survival probability. Data suggest that the low number of recruits from philopatric females was related to costs of inbreeding. The low LRS of long-distance dispersing females may have resulted from their offspring being especially prone to disperse outside the study area, but also other potential explanations exist, such as local maladaptation.

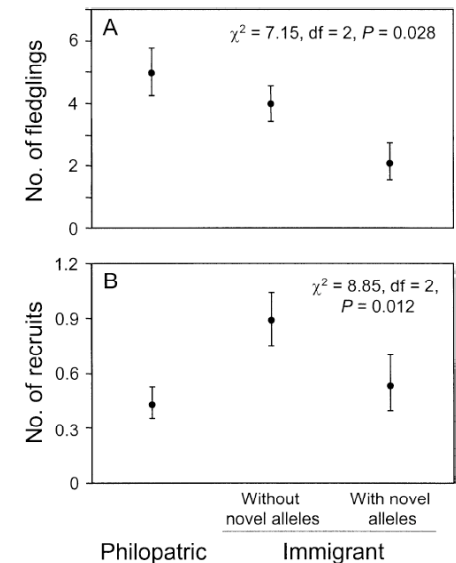


Figure 12.6. Number of fledglings in males ($n = 141$), and (B) number of recruits in females ($n = 156$) for the greater reed warbler, *Acrocephalus arundinaceus*. (from Hansson et al. 2004).

While the study by Hansson et al. (2004) is exemplary in the estimates of fitness, the study does not address the causes of low fitness of males. A study on mate discrimination as a function of distance, within an interbreeding population is required for such inference. The pedigree has superb data on the inbreeding depression experience by philopatric females. Thus, this beautiful example, simultaneously illustrates the principles of inbreeding and outbreeding depression in action.

A recent study on the song sparrow, *Melospiza melodia*, illustrates that mate discrimination based on dialects is likely, especially for female birds (Searcy et al. 2002). Female song sparrows showed preferential response to local songs over foreign songs recorded just 34 km distant. Males did not show a significant difference in response to local and foreign songs except in tests using foreign songs from the end of the transect, at a distance of 540 km. Therefore at least females are discriminating against long distance dialects (Fig. 12.18).

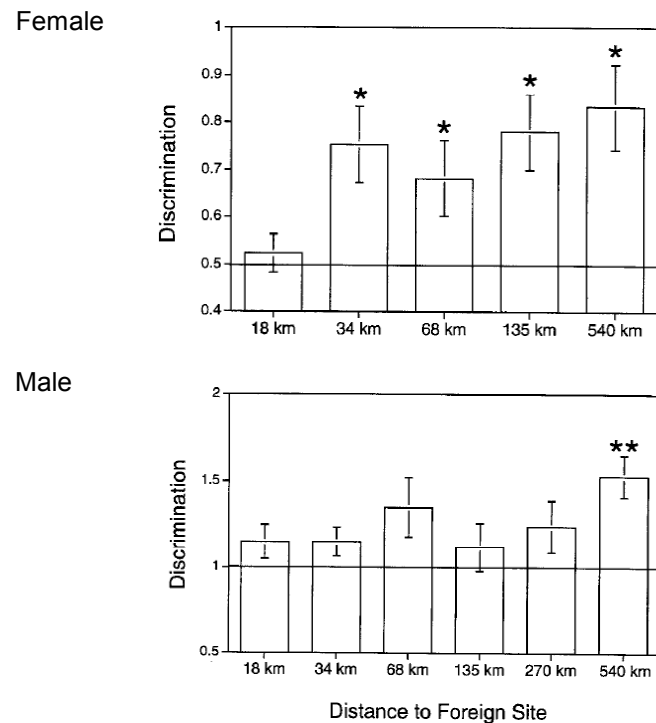
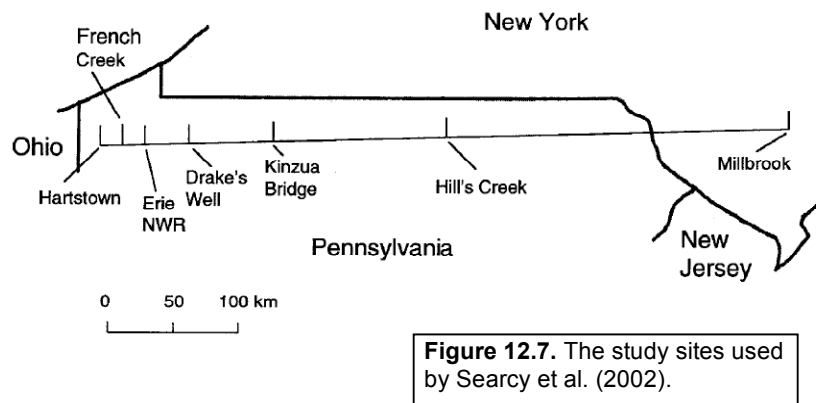


Figure 12.8. Discrimination of mates in each sex of song sparrow, *Melospiza melodia*, based on playback studies. (Searcy et al. 2002).

Extinction, Colonization Success and Dispersal

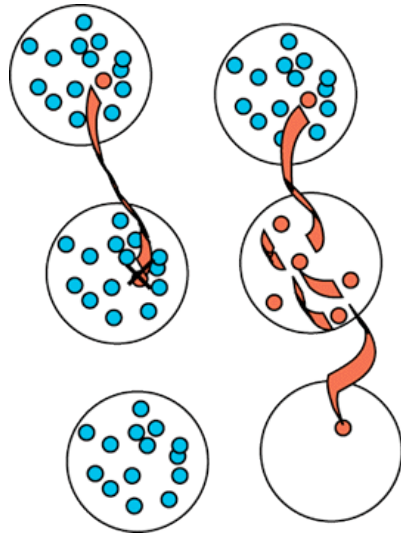
The advantages and disadvantages of dispersal strategies are not limited to genetic costs of inbreeding. Consider, a meta-population in which many sub-populations are found loosely connected and each sub-population is relatively small. Moreover, each sub-population has a modest probability of **local extinction** where all members of the population might be eliminated by some random environmental disaster.

In such a case, selection will favor individuals that disperse from occupied habitats to those parts of the habitat where a local extinction has occurred. Such **disperser genotypes** do not have any inside information about the location of open habitat, but if a lucky disperser happens upon such unoccupied habitat their reproductive rate will be phenomenally high compared to those individuals found in the occupied and crowded habitat. A disperser landing in occupied habitat has low success. Theory predicts that the dispersal tendency will be quite common, even if few dispersers survive, as long as there is a low frequency of extinctions of local sub-populations (Hanski 2000).

The Eastern newt, *Notophthalmus viridescens* appears to be a candidate for an extreme version of this model. An increase in life cycle complexity is exemplified by eastern newts, *Notophthalmus viridescens*, which have an aquatic larval form, a dispersive red eft form, and stream breeding aquatic stage (Pope 1928, Chadwick 1950). Rather than just two body forms (larval, terrestrial adult), the eastern newt has three distinct body forms and behaviors, adding an entirely new phase to the life cycle typical of most amphibians. Thus, eastern newts exhibit a **bimetalphic** life cycle.

The red eft, which is a novel phase, has been inserted into the life cycle. Red efts are protected by striking **aposematic** red coloration, a behavioral signal to deter predation. These juveniles are not just colorful, a signal that deters predators, but also toxic, a physiological adaptation that reinforces the meaning of the signal (Chapter 13). Evolution of aposematic coloration confers red efts with greater dispersal potential than other metamorphic salamander species, which are readily eaten by avian predators if they are exposed in the open.

Figure 12.9. Extinction-colonization in metapopulation. Dispersal is not fit in saturated habitats (left panels), but is in empty habitats (right).



The extinction of newts in a pond is a very likely if adults are not successful in producing metamorphlings across a string of bad years (Gill 1980). Adults breed in temporary ponds, and adults return to the same pond year after year. The reproductive success of newts in any one pond is extremely low, and the newts go extinct in ponds quite frequently. Thus the eastern newt has evolved a dispersing phase to its life cycle called the red eft that wanders around the woods moving great distances over the course of several years of juvenile life. The eft eventually settles in a pond, and if it happens to settle in a nearby empty pond, with at least one mate, the two metamorphosed newts will likely

colonize the pond and have high success from the subsequent growth of their lineage of descendants, and dispersers produced by this lineage that in turn colonize other vacant ponds. The newts appear to be a case in which a new **obligate dispersal phase** has been favored.

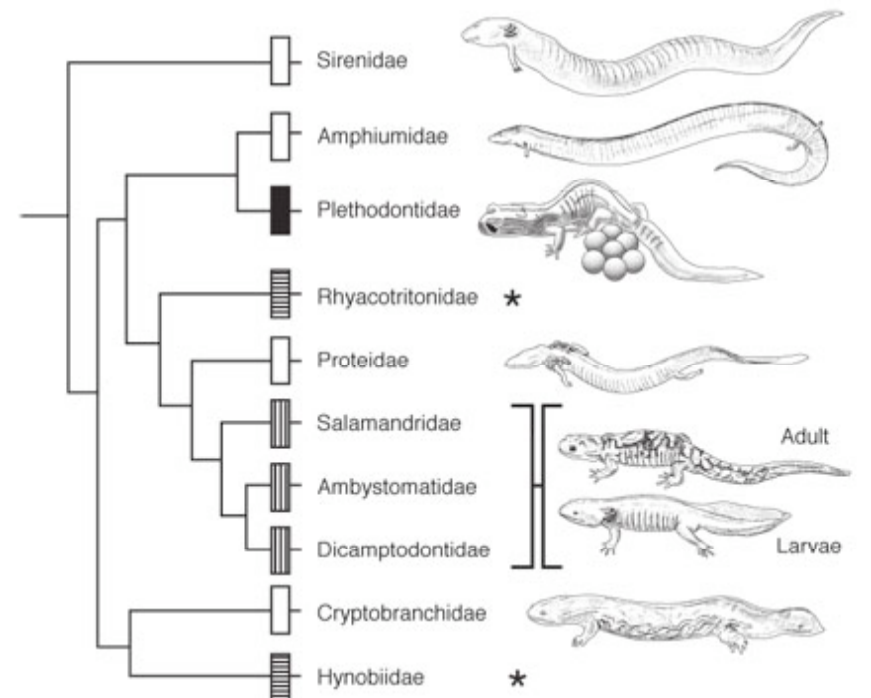
Other species of amphibians illustrate that two or more dispersal types may coexist in the same population. In this case, the dispersal tendency is **facultative** and triggered by density of conspecifics. Semlitch has identified genetic predispositions for two kinds of salamanders:

- 1) metamorphosing from a larva to terrestrial adult, which may or may not come back to breed in the same pond, or
- 2) not metamorphosing and remaining in the pond and breeding in the larval body type.

The type of salamander that does not metamorphose, also does not disperse and is known as a **paedomorphic** salamander. Paedomorphic salamanders remain in the water their entire life. Because they have lost the capacity to metamorphose, paedomorps are susceptible to large-scale

drying events. However, paedomorps avoid the costs of dispersal, they grow more rapidly and achieve a larger size at maturity, and thus gain a competitive advantage over the form that has the typical amphibian metamorphosis and dispersal phase. But in the evolutionary long term paedomorps are doomed to extinction. Even if the paedomorphic form goes extinct, the metamorphic form will re-colonize the pond. New paedomorphic mutants are probably arising all the time. The evolutionary switch or mutation that gives rise to new paedomorphic forms is simple. All that is entailed is down-regulation of genes that

Figure 12.10. The families of salamanders with open boxes indicating obligate paedomorphs, shaded boxes indicating plasticity within species or variation among species, and solid indicating the evolution of direct development (no aquatic larvae). Groups without paedomorphosis are given in horizontal hatching. This is a classic case of **convergence** in which the same adaptation has evolved repeatedly over the course of evolutionary divergence (Chapter 18 provides more on convergence). One group, the plethodontids have evolved direct development and eliminated larval phases in some, but not all genera.



trigger metamorphosis from aquatic larvae to terrestrial adult (Side Box 12.1). The other more typical metamorph possesses fully functional genes and metamorphoses under most conditions. This form is likely to colonize any newly extinct ponds. In the long term, it has an advantage over the paedomorphic form because all ponds will eventually dry up and the populations will go extinct. Because new paedomorph mutation will always arise and invade it is an excellent example of a system that has no [Evolutionarily Stable Strategy](#). Both forms coexist, but one form periodically outcompetes the other, yet neither is a long-term winner.

Migration, Orientation, and Navigation

As noted above, **Dispersal** is typically associated with a once in a lifetime event -- movement to a new habitat. During the dispersal event, it is thought that animals might make a random movement, and then settle once suitable habitat is found. Once the animal has settled in a suitable patch, it must move around its local universe and not get lost.

We will explore how bees and birds use visual cues such as the sun or the stars to orient. We will consider magnetic navigation in birds. **Orientation** is the use of external cues to move about the environment. Orientation can come about by fixing a position and then using cues to determine the appropriate direction to move in. **Navigation** involves a little more sophistication in that a map sense (a sense of where you are) in addition to a compass sense (a sense of the appropriate direction in which to move) is a requirement for a complete navigational system. Many studies have demonstrated orientation, but few have demonstrated that animals have a *map sense* or a sense of where they are (but see Phillips et al. 1995 for a newt example, and Boles and Lohman for a lobster example 2003, which is discussed next).

True navigation

An animal can be considered to have **true navigation** if, after displacement to a location where they have never been, they can determine their position relative to a goal without relying on familiar surroundings, cues that emanate from the destination, or information collected during the outward journey (Griffin 1952, Phillips 1996, Boles

and Lohmann 2003). Boles and Lohmann (2003) displaced spiny lobsters, *Panulirus argus*, 12-37 km to unfamiliar locations and observed their remarkable ability to orient back to their site of capture, even when they were deprived of all known orientation cues *en route*. They also tested the hypothesis that lobsters derive their positional information from the Earth's magnetic field. Lobsters were first captured and then tested for navigation. Lobsters tested in a field north of the capture site oriented themselves southwards, whereas those tested in a field south of the capture site oriented northwards (Fig 12.11). Navigation also occurred if the lobsters were subject to magnets during transport (but not during testing, Fig. 12.12). Their results imply that true navigation in spiny lobsters is based on a magnetic map sense.

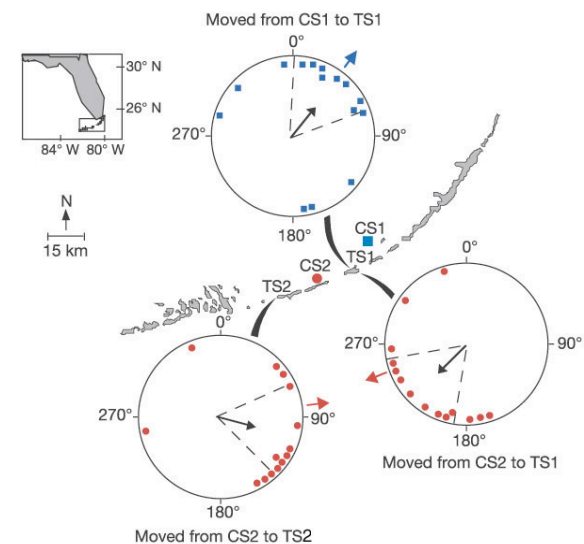


Figure 12.11. Lobsters were transported by boat from two capture sites (CS1, CS2) via circuitous routes to one of two test sites (TS1, TS2). In the orientation diagrams, each small symbol represents the mean angle of a single lobster. Blue squares indicate lobsters captured at CS1, whereas red circles indicate lobsters captured at CS2. Dashed lines represent the 95% confidence interval for the mean angle. Data are plotted relative to magnetic north. The blue or red arrow outside each orientation diagram indicates the direction from the test site to the capture site. In each case, the mean angle of orientation coincided closely with the direction towards the capture site and the 95% confidence interval encompassed this 'homeward' direction. (Boles and Lohmann 2003).

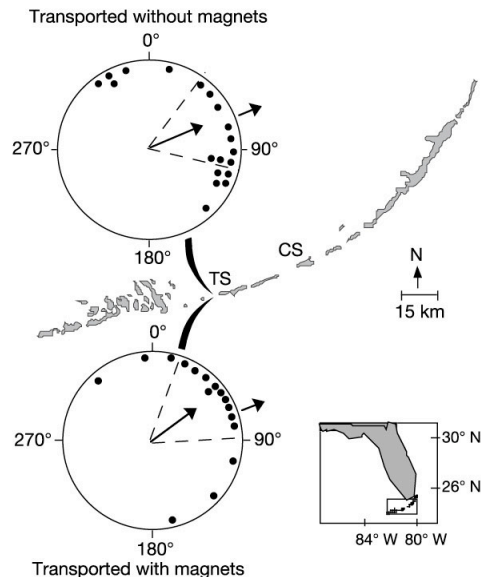


Figure 12.12. Lobsters in a 2nd experiment were collected from one site (CS) near Long Key and transported to a test site (TS). One group of lobsters (upper diagram) was subjected only to the magnetic field distortions produced by the metal body of the transport boat. The second group (lower diagram) was subjected to stronger, additional field distortions caused by stationary and moving magnets. The arrows outside each orientation diagram indicate the direction from the test site to the capture site. The two distributions were not significantly different; instead, both groups of lobsters oriented themselves approximately towards the capture site (71°). (Boles and Lohmann 2003).

Migration

Migration is distinct from dispersal in that migratory animals typically move from one geographic region to another without using the intervening habitat. Navigation is key to orientation and migration. Migrations are associated with specific seasons, and tied to reproduction and endocrine system. A key issue underlying migration is how animals navigate the huge distances or orient to natal areas. Underlying most migrations is a sense of **time** so that the appropriate season for migration is used. Migration is classically associated with birds. However, many other groups undertake long migratory movements:

1. insects (e.g., Monarch butterflies),
2. mammals (caribou, wildebeests, whales),
3. amphibians (e.g., newts to their natal pond),
4. reptiles (e.g., sea turtles),
5. birds (famously migratory)
6. fish (salmon, eels)
7. Humans: The Sami, the people of northern Finland, Norway, Sweden, Russia) that migrate in conjunction with their migratory herds of caribou. (also true in Mongolian cultures).

The Hormonal trigger for the initiation of migration

Migratory behavior is triggered by seasonal photoperiodic cues. Cues are integrated by centers in the brain (the parietal), which induces secretion of hormones that triggers migratory movements. In amphibians this movement is called the **water drive**. In experiments very similar to the lobster studies, Phillips et al. (1995) demonstrated that newts also use a magnetic field to move to and from their breeding ponds. The migratory behavior of all vertebrates, if present, and care-giving behavior of vertebrates has its origins in the water drive of amphibian migration (Rankin 1991; Schrader and Anzenburger 1999). A phylogenetic analysis of the evolution of endocrine regulation in amphibians enriches our understanding of trade-offs and the origins of behavioral traits like migration and maternal care in other vertebrates. In all vertebrates, migration is controlled by prolactin. In addition, if parental care is present, this is likewise controlled by prolactin. Thus, migration and parental care are often coupled in a given life history, largely because of the regulatory effect of prolactin on both behaviors.

The genetic and endocrine triggers of migration

The gene that short-circuits migratory ability altogether (e.g., adults never metamorphose and move away as juveniles) has been mapped to a deletion in a locus that controls thyroid hormones, (Voss and Shaffer 1997), which interacts with prolactin (Side Box 12.1). To map this gene, Voss and Shaffer (1997) crossed paedomorphic Axolotls to ancestral metamorphic *A. tigrinum*, and used linkage maps to track associations of marker loci with expression of paedomorphosis in F1 and F2 progeny.

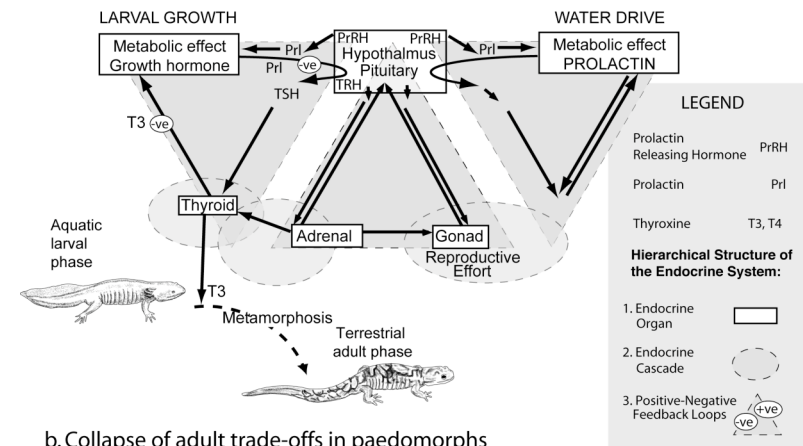
Side Box 12. 1. Endocrine control of migration and parental care

Many physiological functions of vertebrates are controlled by the **Hypothalamic-Pituitary (HP)** gland, which involves a series of endocrine cascades such as those governing reproduction (e.g., central triangle in panel a). The **HP-Gonadal-Adrenal** axes interact to achieve organismal homeostasis during reproduction via *positive and negative feedback* (Chap. 8, Fig. 8.10). Migration and parental care (if present) are also controlled by a system of positive and negative feedback involving prolactin (right triangle in panel a). Moreover, the trigger for the initiation of metamorphosis, the first event that leads to migration from the pond, is governed by prolactin-thyroxine feedback loop (left triangle, a).

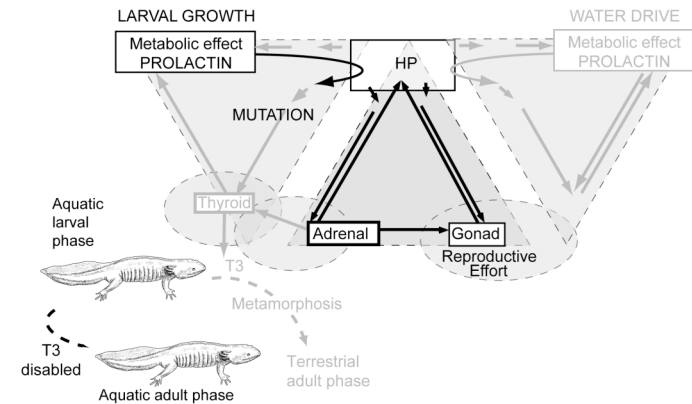
Endocrine regulation can be visualized as interacting endocrine axes (one side of each triangle), which complete a network of *positive and negative regulation* (1 triangle). The hypothalamic-pituitary (HP) organ is a master regulator of endocrine regulation in all vertebrates (triangle apex). A generic complex life history for salamanders is depicted (*Ambystoma* spp.) and the HP-thyroid-growth hormone axis regulates metamorphosis (see Chapter 2, Side Box 2.6), while the HP-gonadal-adrenal axes regulates reproduction (see Chapter 8, Figure 8.10). In terrestrial adults, the HP-prolactin-growth hormone axis further regulates a behavior called **water drive**, which induces adults to migrate back to water and to reproduce. Prolactin modulates migratory behaviors in all vertebrates (Rankin 1991). As with all protein hormones produced by the hypothalamic-pituitary system the system includes a coupled set of hormones a *releaser* and a *stimulator* (e.g., GnRH, FSH or TRH, TSH). Prolactin releasing hormone (PrRH) triggers the release of prolactin (PrI), which travels to targets throughout the body, but in particular interacts with growth factors, since PrI is a growth factor analogue. Migration distance from the breeding site generates life history tradeoffs. While the distance of migration alleviates local crowding around a pond, a long migration may lower adult survival, another life history trade-off. The same life history trade-offs apply to migratory birds, and mammals, though the spatial scale of migration might be quite different.

Loss-of-function mutations at different points along the regulatory pathway of the HP-thyroid axis have given rise to all of the families of paedomorphic salamanders depicted in Figure 12.10 Deletion of the adult phase (via a simple loss-of-function mutation in the thyroid hormone pathway has given rise to the Axolotl. Conversely, deletion of the larval phase has given rise to direct developing plethodontid salamanders. In vertebrates, prolactin also regulates expression of parental care (Schrader and Anzenburger 1999). Given the absence of strict water drive in terrestrial plethodontid species, prolactin machinery has likely been co-opted for a novel function such as maternal care (e.g., observed in *Ensatina eschscholtzii* salamanders). Female *Ensatina* salamanders guard their eggs and secrete substances on their skin that is applied to eggs, which inhibits fungal growth. It should be noted that in birds and mammals prolactin is the trigger for parental care as well as migratory behavior.

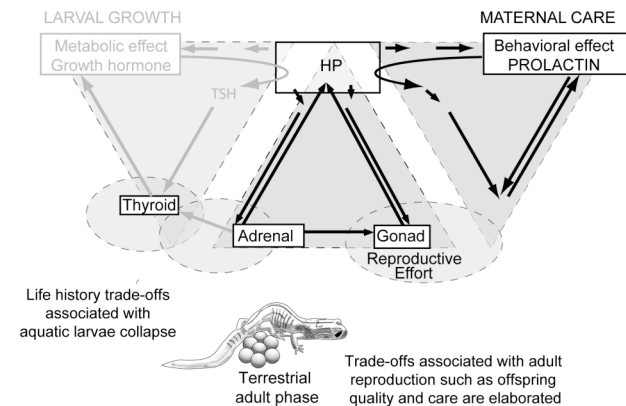
a. Ancestral Complex Metamorphosis



b. Collapse of adult trade-offs in paedomorphs



c. Adult Trade-offs Associated with Direct Development



Paedomorphosis, a recessive trait, is absent from the F1, but is reconstituted in F2 homozygotes, and its transmission is linked to one marker (Voss and Shaffer 1997). This deletion makes it impossible for later migratory events to be triggered, thus, the mutation extinguishes the action of other systems that control migration (Box 12.1). This kind of mutation is likely to be generic in species that evolve philopatric behavior. For example, many bird populations have evolved philopatry in various parts of the species range. When it is possible for the birds to overwinter safely at the breeding location, without having to undergo costly migration closer to equatorial habitats, philopatry readily evolves.

The genetics of migratory direction

The best examples of a genetic basis for migration are derived from studies of avian migration (Berthold 1988, Berthold and Pulido 1994) and insect activity, wing morphs, and flight duration (Roff and Fairbank 2001). In insects, activity, wing morphology and flight duration are not necessarily linked to dispersal ability since dispersal requires appropriate morphology and physiology as well as behavioral adaptations (e.g., decision to leave and settle).

Moreover, factors operating in insects are not necessarily the same as those at work in avian migration (Belluere et al. 2000). This might explain why genetical studies of movement in *Drosophila* spp., a dispersal behavior, have yielded contradictory results depending on experimental conditions and the traits scored (Connolly 1966, Van Dijken and Scarloo 1980, Roff and Fairbank 2001). As noted above, dispersal is a complex behavior controlled by both maternal hormones and genes. Migration has a far simpler and much more targeted effect that moves animals to and from one specific location to another.

Avian migration and navigation: *Zugruhe* response

How do we assess the cues that birds use for orientation? Birds indicate the direction that they wish to fly by a well-known phenomenon called the *zugruhe* or nighttime restlessness (Fig. 12.13). ***Zugruhe*** refers to the sharp jump in nighttime activity that occurs at the onset of the migratory response. Because birds migrate at night, but are not normally

active at night during other times of the year, students of navigation have used birds as a model system for understanding directional orientation. Another aspect of *zugruhe* is that birds orient strongly in the direction in which they are to migrate. A clever apparatus consisting of a cone shaped cage with a mesh top (Emlen 1970), and an inkwell at the bottom has been developed to record the directionality of the *zugruhe*. The birds hop up and down trying to take flight, and end up leaving a complete record of each hop, as well as the direction of the hopping relative to magnetic north. In the example of black cap migration (above), the researchers used the *zugruhe* response and the Emlen funnel to determine genetically predetermined migration directions of fledged young.

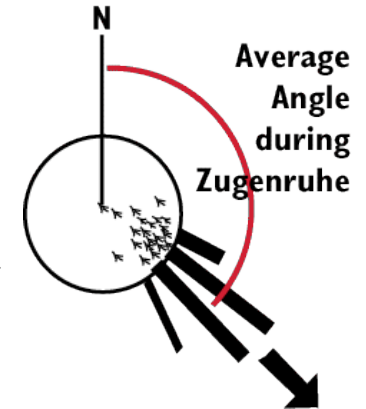


Figure 12.13. Average angle during *zugruhe*, recorded on an Emlen funnel is the basic test for migration direction (usually in fall) in naïve birds.

Migratory routes in European birds

Black caps, *Sylvia atricapilla*, use two migration routes to move from Europe to Africa. These are migration routes used by most songbird species that migrate from Europe at the end of the summer to Africa, and back the following spring. The routes are so popular with birds that raptor predators, which specialize on birds, station themselves at the migration corridors in the fall and pick off migrating birds. The other option is traverse the Mediterranean, but this path is riskier so most birds opt for east or west land routes.

What happens when you hybridize birds from either side of the migratory range? If you take adult black caps from each side of Europe into the lab and cross them in the lab, the F1 hybrids exhibit an intermediate migratory direction (e.g., western migratory route × eastern migratory route). What happens to F1 birds in nature? Will this yield speciation?

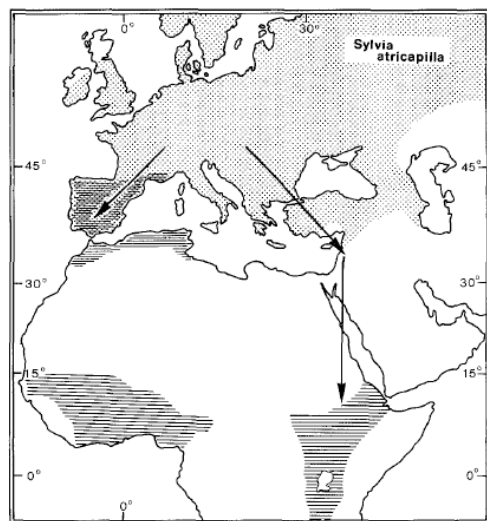


Figure 12.14. Breeding (stippled) and overwintering habitat of the blackcap.

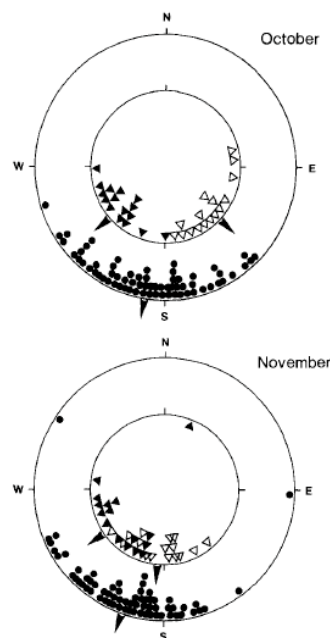


Figure 12.15. Directional choices of hand-raised blackcaps during the early and late part of the autumnal migration. Inner circle parental generation (solid triangles, birds from Germany, open triangles, birds from eastern Austria). Outer circles (full dots, F1 generation) (Heldig 1996).

Heldig's (1996) elegant breeding studies on black caps demonstrate that a simple genetic switch governs migratory direction in naïve birds (Figure 12.14-15). Hybrids are intermediate from either of the two pure parental populations from Germany or Austria.

The difference in migration routes between black caps in western *versus* Eastern Europe is also observed in many other species of birds. Recoveries of ringed birds (e.g. Zink, 1973–1985) indicate that such migratory divides are fairly sharp in white storks and blackcaps, as well as the white wagtail *Motacilla alba*, the bluethroat *Luscinia svecica*, and the willow warbler *Phylloscopus trochilus*. Selection pressures leading to such behavioral differentiation are determined by the costs of migration (in terms of distance and difficulty of crossing an ecological barriers) and geographical distribution of appropriate wintering habitats (Lundberg and Alerstam, 1986). For European migratory birds, the Alps, the Mediterranean Sea and the Sahara Desert combine to create a formidable topographical and ecological barrier. It is advantageous to

deviate either towards the east or west, rather than take the great circle route over open sea, peaks and desert, to the intended winter habitat.

Another remarkable fact is that a recent evolutionary change in migratory direction of blackcaps has been brought about by climate change (Berthold et al. 1992). During the 1990's, a fraction (7-10%) of the ring recoveries of black caps from Belgium and Germany end up in Great Britain, where this sub-group of black caps overwinter. This change in patterns of migration is actually very recent. Before 1960 the number of wintering black caps in Great Britain was essentially zero. Helbig et al. (1994) brought a sample of birds from Britain, raised progeny from the birds and tested progeny against a group of controls from southern Germany. The birds from Britain had indeed evolved a W-NW migration route, within 40 years, presumably in response to the ameliorating climate in Great Britain. Global warming, an inconvenient truth is the obvious candidate for shifting in migratory patterns of birds.

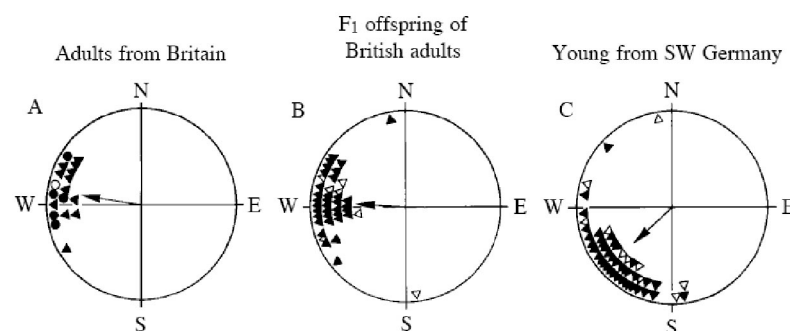


Figure 12.16. Orientation of blackcaps caught in winter in Britain (A), their captive-bred F1 offspring (B) and a control group from southwest Germany (C). In A, triangles show vectors for birds that are parents of F1 offspring. (from Berthold et al. 1992; Helbig et al. 1994).

Notice that their crosses imply that a simple dominant mutation might be enough to trigger the genetics of migratory direction in the case of the route from Germany to Great Britain (Fig. 12.16). A single copy from the mother yields a migration to Great Britain, when crossed to German with SW migration. The studies do not address the actual cues used, but a large body of evidence (Able 1991, 2001) suggests that some cues must be magnetic in nature. Researchers have even traced the mechanism of magnetic orientation to vision (Side Box 12.2).

Side Box 12.2. Birds 'see' the magnetic lines of force

Theoretical, behavioral and physiological evidence supports two magnetic sensing hypotheses: a *magnetite-mediated magnetic sense* (Walker et al. 1997; Kirschvink et al. 2001, Fleissner et al. 2003) and/or a *vision-mediated magnetic compass* (Ritz et al. 2000). The magnetite-mediated mechanism seems to act as part of a magnetic map-sense (see lobsters), which could provide the animal with information about its geographic position, whereas the vision-mediated magnetic sense seems to be a pure compass sense that is based on radical-pair processes in the birds' eye(s). Together the systems can confer true navigation. The light-dependent magnetic compass hypothesis suggests that magnetic modulations of radical-pair processes in photoreceptor molecules in the birds' eyes provide orientation by sensing magnetic field lines. Putative sensor molecules (cryptochromes), which possess the required biophysical properties, are expressed in the retina of migratory birds (Möller et al. 2004, Mouritsen et al. 2004). In garden warblers, *Sylvia borin*, the retinal ganglion cells, which express cryptochrome, along with a neuronal cluster called "Cluster N", which is located in posterolateral regions of both forebrain hemispheres, show high neuronal activity during *zugenruhe*. The expression of the gene ZENK turns on and off during night *versus* day to confer magnetic orientation (Fig. 12.17). Heyers et al. (2007) found that Zenk and other neuronal markers to trace back to two distinct start points, one from Cluster N and the other from the eyes back back the specific parts of the visual thalamus called the dorsal geniculate complex (Gld) (Fig. 12.18). Thus, the two areas of the central nervous system that are most active during magnetic compass orientation are part of an ascending visual processing stream referred to as the thalamofugal pathway. Furthermore, Cluster N seems to be a specialized part of the **visual wulst**, which is dedicated to a magnetic compass sense.

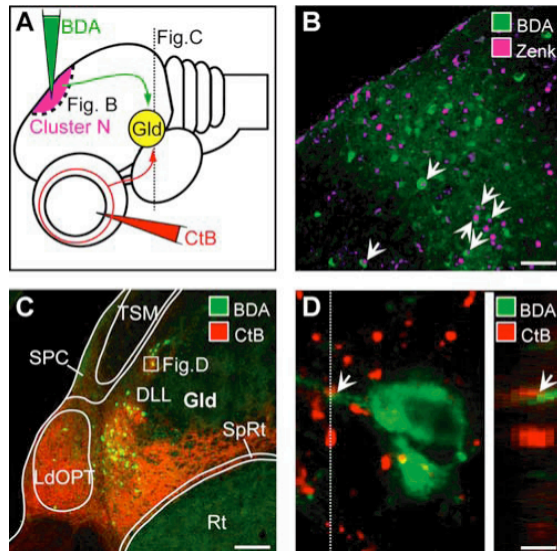


Fig. 12.18. Neuronal tracing, a technique in which neurons are injected with a label (BDA injected into panel A) or a second label (CtB into the eye, pane A), reveals that Cluster N receives input through the **thalamofugal visual pathway**. A) Schematic side view of the bird's brain indicating the locations of tracer application. Retrograde tracer (BDA, shown in green) was applied into Cluster N (magenta). Anterograde tracer (CtB, shown in red) was injected into the vitreous of the contralateral eye. B) Double-labeling of ZENK and the retrograde tracer BDA in sagittal brain sections at the level of Cluster N proves the correct placement of tracer into Cluster N: arrows point to examples of neurons displaying ZENK-expression (magenta) in the nucleus together with BDA (green) in the somata. Scale bar: 25 mm. C) Tracer distribution in frontal brain sections at the level of the thalamic Gld. Labeled fibers from the retina (in red) project upon all components of the Gld, i.e., LdOPT, SpRt and lateral/ventral parts of the DLL. Labeled neurons projecting upon Cluster N (visualised in green) mainly originate within the DLL, with few additional connections from the LdOPT and SpRt. Scale bar: 50 mm. D) Confocal 3D-stacks in the thalamic Gld at high magnification indicate direct contact (arrows) between retinofugal fibers (in red) and somata/proximal dendrites retrogradely labeled from Cluster N (shown in green). Scale bar: 4 mm. Abbreviations: DLL, Nucleus dorsolateralis anterior thalami, pars lateralis; Gld, dorsolateral geniculate complex; LdOPT, Nucleus lateralis dorsalis nuclei optici principalis thalami; Rt, Nucleus rotundus; SPC, Nervus superficialis parvocellularis; SpRt, Nucleus suprarotundus; TSM, Tractus septomesencephalicus. (Heyers et al. 2007).

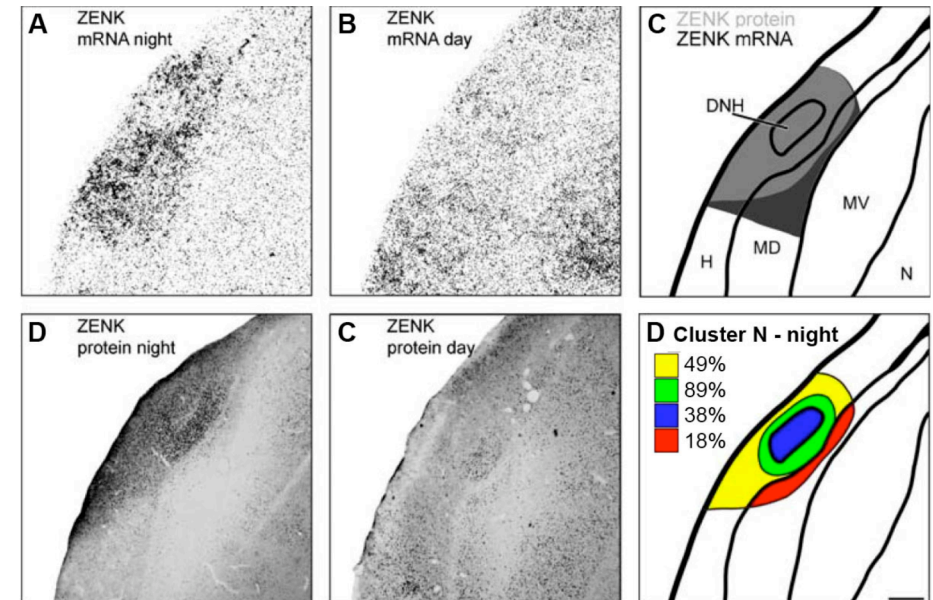
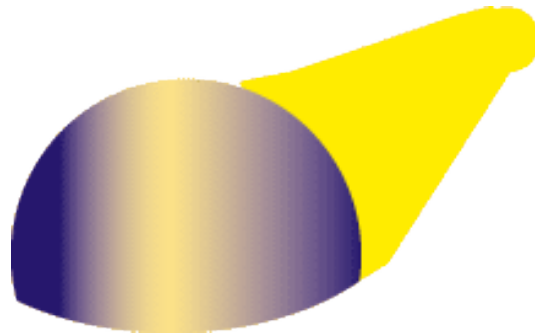


Fig. 12.17. Quantification of ZENK mRNA expression and comparison of ZENK protein within Cluster N. A) Expression of ZENK mRNA during nighttime *zugenruhe* covers posterolateral parts of the hyperpallium and underlying mesopallium of Cluster N, compared to B) daytime expression. D) Expression of ZENK protein during night-time covers hyperpallial compartments, compared to D) daytime patterns. E) Patterns of Zenk mRNA and protein are comparable during night. F) Within the center of Cluster N, c. 56% of neurons show nuclear expression of ZENK protein with highest relative amounts of ZENK-positive nuclei (89%) in the shell surrounding the DNH nucleus. Scale bar 250 mm. Abbreviations: DNH, dorsal nucleus of the hyperpallium; H, hyperpallium, MD, dorsal mesopallium; MV, ventral hyperpallium; N, nidopallium. (from Heyer et al. 2007).

A Celestial Compass

A pervasive feature in the environment that animals could use for orientation is the sky itself. The sun rises at specific times during the day, and provided that an animal has a sense of time, the relative position of the sun could be used to determine direction. However, cloudy skies limit the use of the sun as a source of orientation information. What remains intact on even the cloudiest of days is polarized light. Light rays entering the atmosphere become scattered. Owing to physics, this creates polarized light. The sky in the direction of the sun is less strongly polarized than the sun in the other half of the sky, which is maximally polarized -- even on a partly cloudy day. Of course a cloudy day does obscure the polarization quite a bit, but it still remains a steady albeit attenuated environmental cue that could be used as a directional cue provided that organisms could detect polarized light.



Anti-solar sky **solar sky**
Figure 12.19. Visualizing polarized light.

What is polarized light? This is tough to visualize. Well imagine you had eyeballs sensitive to polarized light and you looked at the sun (Fig 12.19). The light from the sun is coming from all directions and is not all that polarized, so the sun would look dark (called solar sky). As you turn your head away from the sun and look 90° away, the polarized light gets brighter and brighter. Exactly 90° away polarized light is at its brightest because many light rays are heading perpendicular to your field of view. As you continue turning your head, further away from the sun, the polarized light gets dimmer and dimmer, until it is dark again when you are looking away from the sun (called the anti-solar sky). This is because light is heading away in all directions compared to when you are looking 90° from the sun, when light is coming from the sun perpendicular to your viewpoint.

Bees and Polarized Light

The celestial compass of bees was discovered by somewhat indirect means. Bees go out on foraging flights, find food, and then fly back to the hive to communicate to the other workers the source of the food. The bees use a waggle dance to indicate the direction of the nectar source. The sun provides a very constant reference in the sky for the bees to direct other workers. The bee ends its circuit around the loop with a waggle, and the distinctive waggle part of the dance lines up with a vector that leads directly to the nectar source (Fig. 12.20). Distance from a hive is proportional to number of waggles in the dance.

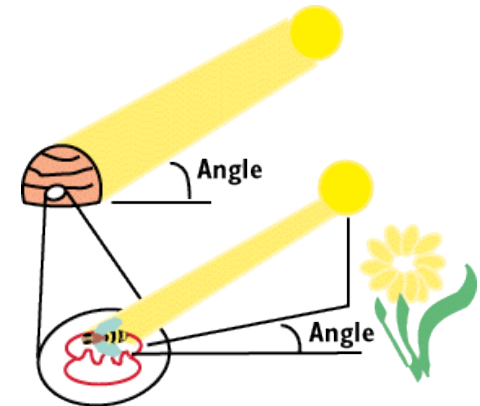


Figure 12.20. The waggle dance of the bee, measured as an angle from the food source relative to the sun's rays (of polarized light).

Karl von Frisch decoded the language of bees using some clever manipulations. The tendency for bees to point in the correct direction of the nectar supply can be plotted on a circle. The height of the histogram is proportional to the number of worker bees that choose that vector (i.e., typically close to the actual angle of the plant from the sun if they are correct). Few workers are far off the actual angle. In the diagram to the right, the average angle of that the forager bees take relative to the angle of the scouts waggle dance, indicates that food is located approximately 100° to the right of the sun (Fig. 12.21). A forager would fly at a bearing of 100° from the sun and come upon the source of food that the scout bee had found. It appears that the forager is using the sun a reference. In actuality the bee is using polarized light as a reference. The ommatidia of

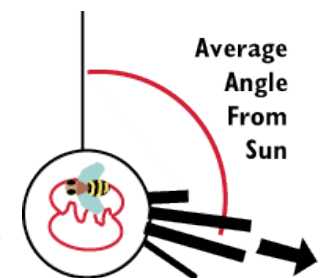


Figure 12.21. Angle of the waggle dance (100°) relative to sun's rays that is communicated by a returning scout to a forager (see text).

the bee contain special photoreceptors that are sensitive to polarized light in ultraviolet wavelengths.

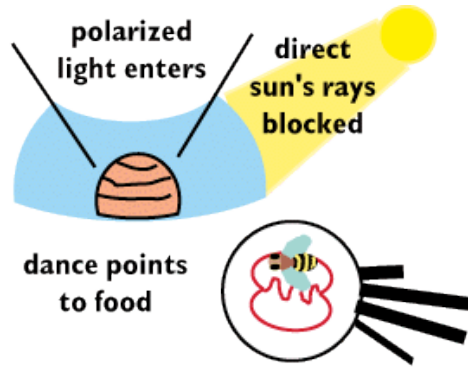


Figure 12.22. Eliminating direct sunlight, but allowing in polarized light has no effect on the correct waggle angle by the scout.

of screen. Scouts display the correct angle to nectar, even though the sun is not visible, and foragers fly in the right direction (Fig. 12.22).

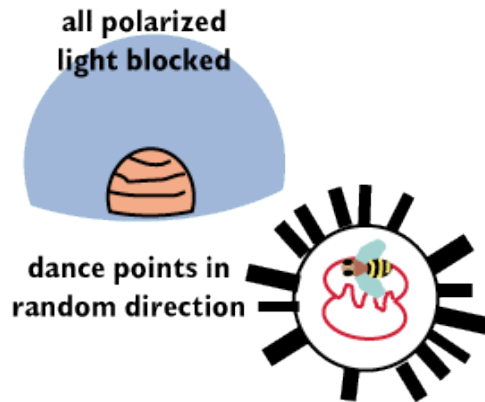


Figure 12.23. Eliminating polarized sunlight, but allowing sunlight, yields random patterns.

a random pattern (Fig. 12.23) compared to the correct direction for foragers with polarized light (Fig. 12.22).

Wehner and Rossel (1987) uncovered the workings of the bee's celestial compass by manipulating the kind and wavelengths of light coming into the hive while the scout bee did its waggle dance. They showed that the sun's rays were not necessary by putting up a screen that eliminated the sun's direct rays from entering the hive, while permitting the sky's polarized light to reach the hive through an opening in the top

If you block out all polarized light using a Plexiglas bubble, you eliminate the cue that the bees use to orient. The Plexiglas absorbs polarized light in UV wavelengths. A bee that returns from its scouting knows the correct angle, but without the sun to guide it, the worker cannot use the waggle dance to orient foragers in the proper direction relative to the sun. The data for workers shows a

Finally, one can let in just certain wavelengths of polarized light using filters (Fig. 12.24). In these fine-scale studies, researchers kept altering the wavelengths until they hit upon the exact wavelengths that gave bees the external information needed to orient their dances correctly. Many wavelengths of light gave a random orientation to the dance pattern. However, light in very specific UV wavelengths appears to trigger the polarized light sensitive regions of the ommatidia and allows for correct orientation. In contrast scout bees are "blind" to directional information, if light is in the wrong wavelengths of UV (even if light is polarized).

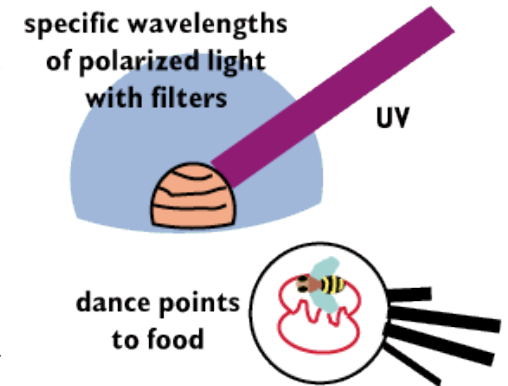


Figure 12.24. If specific wavelengths of UV polarized light are put in the hive for scouts to detect it waggles correctly.

The Sun Compass of Birds

Consider the European starling that has a normal migration route that is in a SE direction (that is it is from the eastern migratory route in Europe). It is easy to shift the direction of *zugenruhe* by using mirrors to alter the true direction of the sun at sunset by 90° clockwise or counterclockwise. Starlings in aviaries that see such a frame-shifted sun end up leaving tracks that are 90° frame shifted in the right direction. The researchers

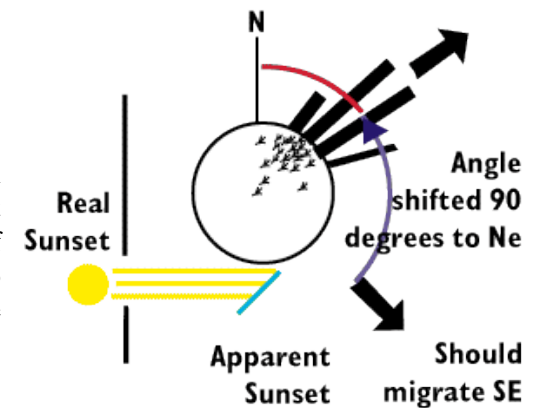


Figure 12.25. A "smoke and mirrors" experiment in which the angle of the real sunset is rotated with a mirror by 90°. This rotates the angle of *zugenruhe* by 90°.

hypothesize that the birds take a bearing on the sun at sunset and then use dead reckoning to fix to set migratory direction during nighttime until sunrise, at which point a new bearing can be used. Regardless of the precise mechanism, it is clear that the birds use the sun as a Celestial compass much like bees used polarized light as a celestial compass.

Overcast Skies

If the skies are overcast (Fig. 12.26), then the birds have a random orientation to their *zugenruhe* movements. This suggests that the sun is necessary to at least get a quick fix on or the birds do not have a directional cue to initiate their dead reckoning during the night. If birds do not have the sun, what other cues might they use? Some have suggested the weather. Winds are very predictable at certain altitudes and a stiff crosswind might be used to aid the bird during periods of no sun or to further refine orientation at night. During the day, birds undoubtedly use large landmarks like the Mississippi River, and such bodies of water would also be available at night via the reflection of the moon. What other cues might birds use at night?



Figure 12.26. In overcast skies when the sun is not visible, a random *zugenruhe* is triggered.

Stellar Navigation: "I got the sun in the morning, the moon and stars at night".

A little primer on stellar navigation

Some birds are real stargazers, and can use the position of the stars to orient. Most of us have looked up in the night sky and you may have noticed that the constellations move during the course of the night. This apparent motion is caused by earth's rotation. Polaris happens to be located directly along the earth's north-south axis. As the earth rotates,

the star Polaris does not move, but the other stars appear to rotate around Polaris, which is the handle-tip to the little dipper.

Planetarium Star Shifts

If birds are set up in a planetarium all of the stars can be projected on the dome like ceiling. The machine that projects the stars on the ceiling can easily manipulate the rotational position of the stars. The orientation angle during *zugenruhe* can be used during such manipulations of stellar cues to determine what information birds might be using at night. First, Sauer simply manipulated the stars images projected on the dome of the planetarium. He rotated the stars by 180°.

The star shift is not just a rotation of the stars (which birds could use as a clock, much like we use the sun during the day), but rather, the orientation of Polaris and all stars around Polaris are flipped into the southern sky. As predicted, he rotated the direction of the *Zugenruhe* by exactly 180° (Fig. 12.27). Birds use some kind of view of the stars to orient their *zugenruhe*.

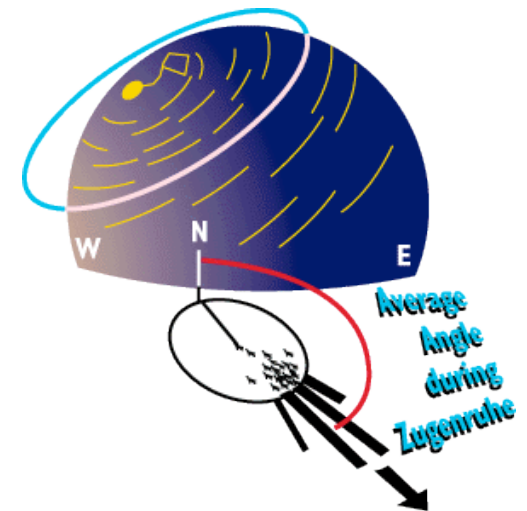
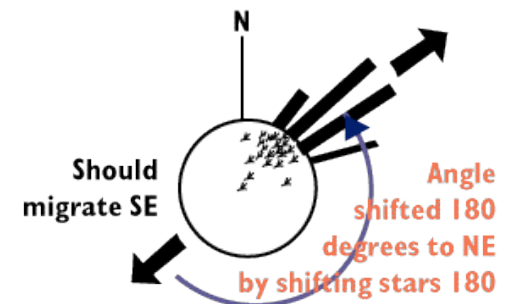


Figure 12.27. A planetarium can be used to rotate the stars in a very natural fashion. In nature, birds will observe the star Polaris as stationary in the sky (above). A planetarium can be rotated around an arbitrary star, 180° from Polaris, which rotates the *zugenruhe*.



Learning or Instinct of the Stars?

Emlen conducted an experiment on the early experiences of Indigo buntings with a star map. He set up three groups of chicks that were reared under the following conditions:

- 1) chicks reared in a room with a diffuse light at night,
- 2) chicks reared with a normal star map that rotates around the north star Polaris,
- 3) chicks reared with a abnormal star map that rotates around Betelgeuse, which is a star on the southern constellation of Orion.

All the birds were then tested with a normal star pattern (even those reared under the baleful eye of Betelgeuse). As predicted, birds without a star chart did not learn the appropriate cues and showed no orientation (Fig. 12.28). Those birds with a reversed experience of the stars also showed a reversed Zugenruhe relative to the control birds. Birds learn the star map as nestlings and use this information to orient their zugruhe.

Use of a star like Polaris, which is the star that does not rotate, is very useful from the viewpoint of long-term changes in our sky map. As the earth rotates its axis actually wobbles and thus the star map is not constant. The axis changes every 13,000 years or so and when it does a different star is rotation center of the nighttime sky.

The other cues used in orientation, such as the magnetic north, likewise change every few millennia. The earth's magnetic pole experiences a huge reversal in polarity, such that north becomes south and south becomes north. This change occurs extremely rapidly and when it occurs nobody knows what consequences it has for the migration of animals. Perhaps those few mutants that normally die when they migrate in the wrong direction are the lucky ones during such events.

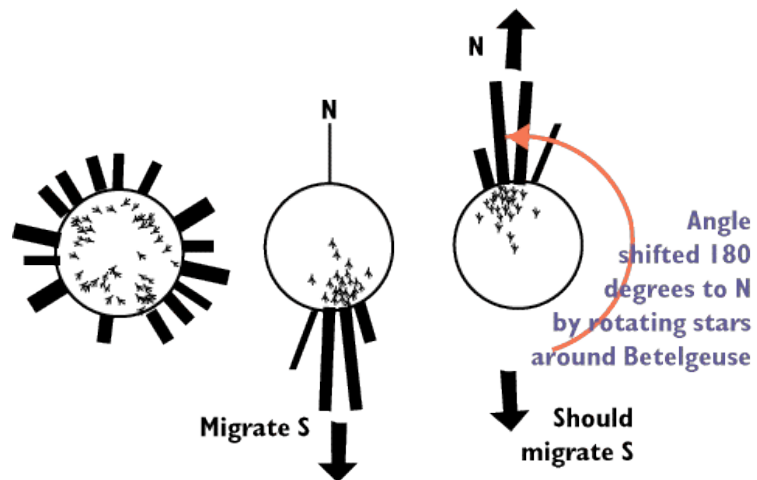


Figure 12.28. If no star is rotated in the planetarium for the naïve fledglings to view, they exhibit a random zugruhe. If the normal Polaris star is used as the rotation point for the sky, where the naïve fledglings spend the night, the exhibit the natural direction – due South. However, if a southern star is chose, in this case Betelgeuse, naïve fledglings have a zugruhe that is rotated by 180°.

Study Questions for Dispersal and Migration

1. Make a distinction between orientation and navigation.
2. Outline the experiments that show [bees navigate by using polarized light](#). How do we know that [they communicate](#) (also, see Adcock)?
3. What is the [zugenruhe](#) as measured in the "Emlen funnel"? What kinds of experiments prove that birds use the [sun](#) or [stars](#) for navigation. Describe the hypotheses and predictions for each experiment. Outline the controls, manipulations, for each experiment.
4. Compare and contrast the [microevolutionary](#) and [macroevolutionary](#) hypotheses describing the maintenance of dispersal tendencies in a population.
5. Can the [macroevolutionary](#) hypothesis of extinction and colonization include a component involving [group](#) selection or perhaps [demic or species selection](#)?
6. Apply the principles of [species recognition](#) (e.g., fitness and natural selection, isolating mechanisms) to the problem of [deme recognition](#) in bird song and song learning.
7. Outline three hypotheses to explain why animals disperse from their natal site. What are the levels of selection that are used in each hypothesis? Provide examples of each hypothesis in action.
8. Describe an experiment that elucidates the genetic basis of dispersal. How can you rule out the effect of maternal effects?
9. Penguins (see March of the penguins) in the Antarctic take on one of the riskiest Migratory marches in some cases moving 70 km on foot to reach solid ground (rather than breed on the ice that cannot sustain the 6 month long nesting period, when the ice melts in the Austral summer. As global warming heats things up do you think that penguins will evolve new migration routes? Describe an experiment that elucidates the genetic basis of migration in another bird and apply it to the penguins.