CHAPTER I: GENERAL INTRODUCTION: COSTS AND BENEFITS OF GROUP-LIVING

All decisions that an animal makes have both costs and benefits. We should expect, however, for the costs to be outweighed by the benefits in order for the behavior (or suite of behaviors) to be considered adaptive (i.e., increase the animals' relative fitness via survival and/or reproduction; Davies et al. 2012). One such decision that animals must make is whether to live in a group. Many animals live a solitary existence; they come together only when necessary (e.g., at concentrated foraging areas or for mating purposes). However, for some species, being around others is integral to their nature.

Group-living is distinct from sociality (sociality implies social interactions among individuals). Although sociality does typically involve group-living, group-living does not necessarily indicate sociality (see Slobodchikoff and Shields 1988; Blumstein and Armitage 1997). Group-living is common in vertebrates: examples of many individuals living together for extended periods of time can be found in fish, birds, and mammals (Rubenstein and Kealey 2010). Group-living is seen outside the Vertebrata subphylum, too, including in ants (Hughes et al. 2002), spiders (Uetz et al. 2002), and brittle stars (Broom 1975). Living in a group should provide fitness benefits for the individuals within that group that outweigh any costs that members incur by joining the group. Examples of potential benefits include: reduced risk of predation, easier access to scattered or uncommon resources, reduced parasite loads, increased mating opportunities, and reduced energy expenditure (Rubenstein and Kealey 2010).

There may be multiple reasons driving the presence of group-living in any animal species. Additionally, there are also notable costs that can be associated with group-living. For example, even though mates might be easier to locate when living in a group, increased competition for mating opportunities can occur (Dobson 1982). While the many-eyes hypothesis

and the dilution effect may explain benefits for grouped animals in avoiding predation, it is also worth noting that large aggregations of animals can also be more conspicuous to predators (Lima and Dill 1990). Two other costs may include increased parasite/disease burdens (Godfrey et al. 2009) and competition for food resources (Majolo et al. 2008). While I will focus primarily on benefits, it is important to acknowledge that many costs may also exist. In reality, adaptive functions of group-living depend on the species' physiology, anatomy, and behavior, as well as the habitat quality, and climate. Below, I review seven common explanations (benefits) for animals to live in groups.

Relatedness and inclusive fitness

An individual can pass on some of its genes, even if it does not produce offspring, by facilitating its relatives' survival or reproduction. In vertebrates, all of an individual's full siblings are as related (coefficient of relationship = 50%) to one another as they would be to their own offspring. Clearly, for more distant relatives (i.e., coefficient < 50%), the fitness benefit is less than if an individual reproduces (i.e., directly passes on genes), but indirectly passing on genes still acts as a net fitness benefit. However, accrued fitness benefits of helping distant relatives could be as valuable as reproducing if the individual helps numerous relatives. Examples include alloparenting of related offspring as in prairie voles (*Microtus ochrogaster*; Stone et al. 2010) or 'self-sacrifice' in some eusocial insects where many individuals do not reproduce—but they exhibit a high degree of relatedness to those that they help reproduce (Queller and Strassmann 1998).

Reduced risk of predation

Individual animals may group together because grouping decreases the chances of predation. This can be as simple as the dilution effect, in which the probability of predation for any particular individual decreases as the group size gets larger (even if the presence of a large group makes detection of the entire group easier for predators). The dilution effect has been used to at least partially explain group-living in many taxa, including stream invertebrates, fish, and insects (Wrona and Dixon 1991; Wisenden and Keenleyside 1995; Creswell 1994). This idea is related to the concept of the 'selfish herd' (Hamilton 1971).

Group-living can more actively reduce predation risk through increased vigilance (e.g., the 'many-eyes' hypothesis) and/or alarm calls. For example, Thomas' langurs (*Presbytis thomasi*) emit alarm calls in the presence of conspecifics when a predator is spotted (Wich and de Vries 2006). Whether group-living yields passive, 'selfish' or more active benefits regarding predation, the benefit should outweigh known costs such as decreased foraging efficiency or increased probability of aggressive or antagonistic behavior from conspecifics (Molvar and Bowyer 1994).

Influence of ecological niche/specializations

Animals may live in groups due to aspects of their ecology: perhaps food is sparse or patchily distributed. Individuals may garner information from other group members that gives them information about foraging sources. Starlings (*Sturnus vulgaris*) were observed to use cues from other starlings regarding the quality of experimentally-placed food resources in deciding whether to visit that patch (Templeton and Giraldeau 1995). For some animals, their environment poses unique challenges which facilitate (or necessitate) group-living. For example, a phylogenetic analysis found that many rodents that reside underground live in groups or have

at some point in their evolutionary history. Generally, group-living is seen in subterranean rodents unless the species developed specialized morphology (e.g., for digging; Smorkatcheva and Lukhtanov 2014).

Reduced parasite loads

It was widely assumed that individuals living in groups would necessarily have higher rates of parasite transmission for both endo- and ectoparasites, although this relationship is perhaps not as strong as previously thought, nor is it universally true (Rifkin et al. 2012). The dilution effect may also apply to mobile parasites. For example, shoaling fathead minnow (*Pimephales promelas*) individuals were less likely to contract trematodes than non-shoaling minnows (Stumbo et al. 2012). However, the dilution effect requires fairly specific constraints and pertains primarily to mobile ectoparasites (like flies) or other parasites which can sometimes be avoided via change in behavior (e.g., some of the shoaling minnows were able to detect and 'dodge' trematodes in the water column). However, the relationship between group-living and vulnerability to parasites depends on both the ecology of the host and the parasite (Monello and Gompper 2010). With parasites that are highly contagious, living in groups is generally a disadvantage (Côté and Poulin 1995).

There is another, perhaps more intuitive way in which living in groups could reduce parasite loads, particularly for ectoparasites: allogrooming. Others can search for and remove ectoparasites in locations on the body which an individual may not be aware of or may be unable to reach. However, benefits of allogrooming may be greater than simply the removal of ectoparasites (e.g., increased social bonds). There are also notable costs to allogrooming individuals. While allogrooming, impalas (*Aepyceros melampus*) become less vigilant for

predators than those not allogrooming (Mooring and Hart 1995). It seems likely that group-living

provides some benefits for parasite avoidance, but these benefits may be outweighed by other

costs in most cases. A notable exception is in leaf-cutter ants (*Acromyrmex* sp.), where a

combination of antibiotic secretions (which increase as ant density increases) and allogrooming

appears to offer substantial resistance to parasitic fungi (Hughes et al. 2002).

Cooperative breeding

Cooperative breeding (i.e., helping rear or provide for offspring) can also occur among

non-related individuals. Assisting with unrelated offspring can be helpful because of a large

benefit simply to living in a group and/or due to experience gained for one's future brood. For

example, pied kingfishers (*Ceryle rudi*s) have been observed to have non-related helpers at the

nest. Non-related helpers do not help as much as related helpers (presumably because any benefit

to being a non-related helper is smaller and less direct), but non-related helpers may have higher

mating success as well as gain experience for the future if they have not reared offspring

previously (Reyer 1980 and 1984).

Reciprocity

Living in groups can also allow individuals to help each other (e.g., during times of

resource scarcity) provided that helped individuals will return the favor at a later date. The

benefit of being helped (even if delayed for the original helper) should outweigh the cost of

helping. A well-known example of this sort of reciprocity has been documented in vampire bats

(*Desmodus rotundus*). In both kin and non-kin, vampire bats have been observed to regurgitate

blood meals for individuals who did not have recent foraging success (Wilkinson 1984). This is

of great benefit to the hungry bat because a few nights without a blood meal (which can be difficult to obtain) can result in starvation. Such systems appear to be relatively uncommon but are robust to 'cheaters' because the animals typically can discriminate between and repeatedly encounter the same individuals. In other words, if a vampire bat accepts help but then does not reciprocate, it should be harder for that bat to receive assistance in the future. Similarly, Thomas' langurs (*Presbytis thomasi*; which I noted earlier as alerting conspecifics to the presence of a predator), appear to remember which individual gave the alarm call (Wich and de Vries 2006).

Thermoregulation and energy conservation

Keeping appropriately warm or cool is important to most animals, whether they are endotherms or ectotherms. Thermoregulation is the process by which an animal uses physiological and behavioral mechanisms to maintain a relatively constant body temperature. When the ambient temperature is near or inside the thermoneutral zone (TNZ) of the animal (the range of temperatures within which an animal's normal metabolic rate is lowest), metabolic energy expenditure required for thermoregulation is lower than in ambient temperatures outside the thermoneutral zone. Animals can use behavioral means to reduce energy expenditure associated with thermoregulation. Such behavioral means may include fanning, panting, shivering, or seeking shade. In environments or microclimates where temperature is substantially outside the thermoneutral zone, these behaviors become very energetically costly (Terrien et al. 2011; Kingma et al. 2012).

Grouping together is another way that animals can regulate their temperatures. Red wood ants (*Formica rufa*) with higher numbers of individuals inside the nest were able to buffer against cool outside temperatures— times when smaller colonies had to wait for exogenous

warming (e.g., high levels of solar radiation on the outside of the nest; Rosengren et al. 1987).

Other examples include alpine marmots (*Marmota marmota*) and Andean toads (*Rhinella spinulosa*), both of which huddle together closely when temperatures are low (Arnold 1988; Espinoza and Quinteros 2008). Grouping together in hotter climates is generally not as helpful for thermoregulating (i.e., cooling off; Dausmann and Glos 2015), but is still useful in warm climates with periodic cool temperatures. For example, red-fronted lemurs (*Eulemur rufifrons*) in Madagascar will huddle together to stay warm during cool nights (cool is relative in this case at < 15˚C). This is in an environment where temperatures during parts of the year can exceed 40˚C (Ostner 2002).

What about bats?

Bats are no exception to group-living: many of the 1,100+ species of bats are highly social and live in large groups (Dechmann et al. 2010). While little data exist for the occurrence of group-living across the entire Chiroptera order, bats that live solitarily are relatively uncommon in the United States. In fact, this feature is a fairly useful identifying characteristic (e.g., Craven and Iwen 1996). Just 25% of the species occurring in Indiana—all of which also occur in Mississippi— are considered solitary (Indiana DNR 2000). Group-living in bats has received less study than many other groups of animals, but numerous ideas have been proposed to explain why bats might live together. Bats may experience many of the potential benefits of group-living covered above: allogrooming (Kerth et al. 2003), information transfer regarding foraging opportunities (Dechmann et al 2009; Wilkinson 1992), food-sharing (Wilkinson 1984), predator avoidance (Russ et al. 1998), and a host of other reasons (e.g., Chaverri and Gillam

2010). Kin selection may also play a role in explaining group-living, although bat colonies often

have low levels of relatedness (Kerth et al. 2002; Rossiter et al. 2002).

Bats and thermoregulation

One of the most important benefits of group-living for bats in temperate locations,

however, is thermoregulation. In endotherms, the body temperature is not generally affected by

the ambient temperature, but ambient temperature affects thermoregulation by influencing the

energy required to maintain the animal's metabolic rate. Thermoregulation requires balancing

heat production by the body with heat loss to the environment; the latter is known as thermal

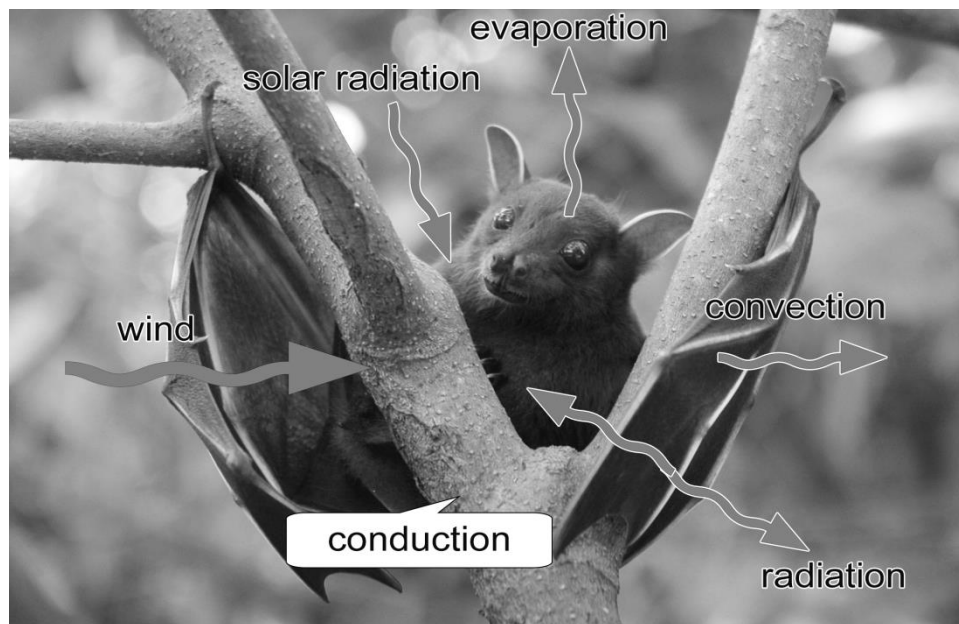conductance (Feldhamer et al. 2003 p. 115; see Figure 1).

Figure 1. Various ways that heat is gained or lost by a bat's body. Note that
conduction (transfer of heat between body and objects in contact) frequently
lowers the body temperature, but if the surface is warmer compared to the body,
the surface can actually warm the body (e.g., a lizard may bask in the sun on a
warm rock). Because they are nocturnal, bats do not generally receive solar
radiation (or substantial amounts of reflected solar radiation). Thermoregulation
via groups (also known as social thermoregulation or 'huddling') reduces
convection because less surface area of each individual bat is exposed to the air.

An animal's thermoneutral zone is the range of environmental/ambient temperatures inside which the body's normal metabolic rate is approximately balanced with thermal conductance. Inside their thermoneutral zone, animals do not have to alter their metabolic rate because they can use behavioral means of increasing or decreasing thermal conductance. Outside the thermoneutral zone, endotherms must increase their metabolism to maintain body temperature. For small animals, this increase is quite energetically costly. Because bats have a high surface area-to-volume ratio, heat loss (i.e., thermal conductance) is a major concern. Bats have a very limited amount of expendable energy, particularly in winter when insects and other seasonal food items are scarce. Couple a temporally-variable food source with bats' energetically-expensive mode of locomotion, small body sizes, and high surface-area-to-volume-ratios, and it becomes clear that energy balance (which is important to all animals) is of paramount importance to bats (Kurta et al. 1989).

In order to survive during periods of low energy intake and high energy loss, bats may seek thermal shelters where they are inactive. In cooler temperatures, bats typically undergo bouts of torpor, a state where the metabolic rate is substantially decreased for several hours to several days (extended torpor is referred to as hibernation). Torpor can reduce the metabolic rate of bats by 15x (Wojciechowski et al. 2007). Torpor allows bats to reduce metabolic upkeep (i.e., reduce heat production by the body that requires energy via food) in the presence of cold air. Cooler air greatly exacerbates thermal conductance (i.e., heat lost to the surrounding environment). One simple proxy for energy expenditure is an animal's heart rate (Weimerskirch et al. 2002). A bat's torpid heart rate can be as low as 10 bpm (beats per minute) despite a normal resting heart rate of 450 bpm and an active rate of 1,000 bpm (Brunet-Rossinni and

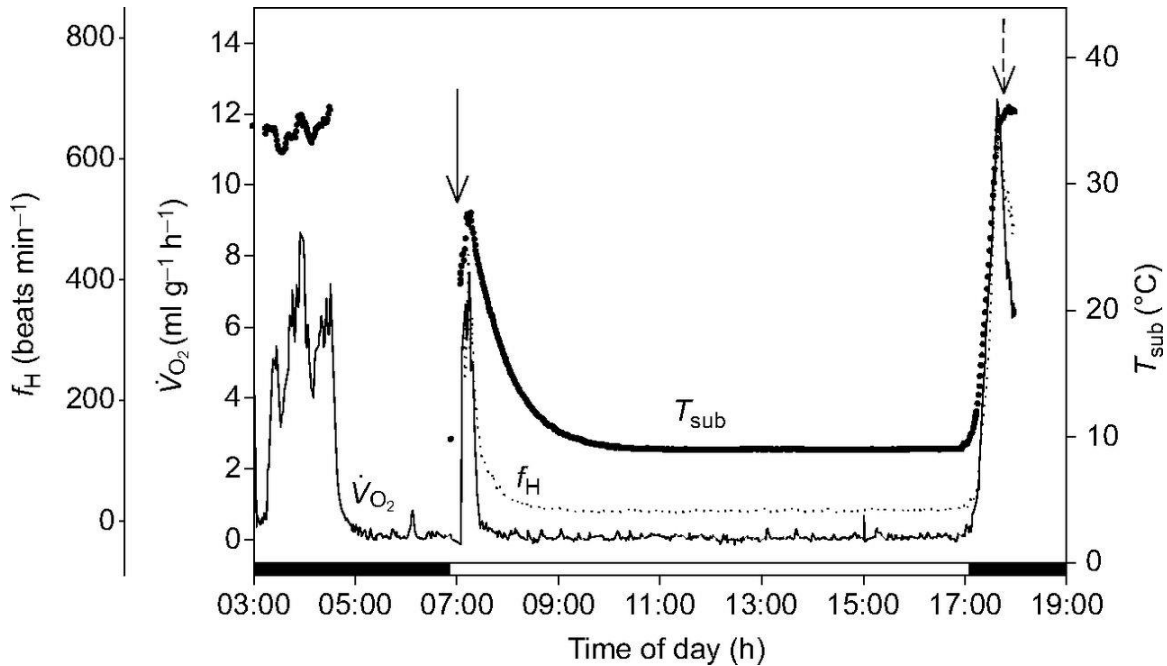Austad 2004). Torpor thus provides a means for reducing the resting heart rate by almost 98% (see Figure 2).

Figure 2. Heart rate, oxygen consumption (VO2), and subcutaneous body temperature of Gould's long-eared bats (*Nyctophilus gouldi*) at an ambient temperature of 10°C. The two arrows represent the beginning and end of torpor. Data and graph from Currie et al. 2014, used with permission.

A downside of torpor is that torpid bats are vulnerable (e.g., to predation or to energetically costly arousal due to disturbance). Therefore, choosing the appropriate location for torpor is of paramount importance. Clearly, temperature and thermoregulation should be the basis for much decision-making in bat species that undergo torpor. A large body of research supports the idea of a relationship between bat behavior and temperature/thermoregulatory needs. For example, use of synthetic bat houses has been linked to temperature regimes. Lourenço and Palmeirim (2004) reported that bats were more likely to use bat houses that had been painted a dark color because these houses had higher internal temperatures. The use of day roosts by female Bechstein's bats was found to be largely explained by temperature. Females

chose cooler roosts before parturition and favored warmer roosts after giving birth (Kerth et al. 2001).

I acknowledge several different potential benefits of group-living in bat species, but thermoregulation is probably the most fundamental. It could be that group-living was initially selected solely as a means of more efficient thermoregulation, and other auxiliary benefits subsequently arose from group-living (exaptations). Some explanations for group-living do not apply very well to bats; bats could probably survive without roost mates alarm-calling in response to predators (Russ et al. 1998) and without other bats recruiting them to a roost (Chaverri and Gillam 2010). However, in environments where temperatures drop below freezing and roosts are not well-insulated from outside temperatures (unlike caves), bats probably require behavioral reduction of thermal conductance. One major way in which this can be possible is through close proximity to other individuals. My research focuses on the ways in which Rafinesque's big-eared bats may use grouping behavior to respond adaptively to thermal and energetic conditions.

Decision processes are an integral part of an animal's life history. An animal responds to stimuli in the environment and should typically change its behavior according to decision rules for a variety of tasks: foraging, avoiding predation, mating, intraspecies conflict, and parental care among others (Feldhamer et al. 2007; Coleman et al. 1985; Enquist and Leimar 1983). A decision simply means that one option is selected from two or more possible 'choices,' although these decisions need not be (and often are not) consciously made.

In behavioral ecology, it is assumed that animals make decisions in an attempt to maximize fitness (i.e., reproductive success or survival) by making trade-offs within ecological constraints (Sih 2013). Identifying and quantifying every piece of information that an animal

could possibly use to make decisions is typically impossible. Moreover, which decision in a particular scenario is most beneficial (in terms of fitness) is not always clear. Despite these difficulties, the study of animal decision-making can be a powerful method to inform evolutionary and ecological theory as well as increase the efficiency and success of conservation and management actions (e.g., see Westneat 2013:275).

Like all animals, bats (Class Mammalia, Order Chiroptera) routinely make decisions. Bats must decide when to enter torpor or hibernation (see Table 1), when and with whom to mate, where to roost, how to navigate the landscape, and where to forage. In each case, multiple options are available to the individual bat.

Table 1. Definitions of common bat biology terms.

torpor	The lowering of body temperature and metabolic rate used to conserve energy. During torpor, bats are immobile.
hibernation	Essentially an extended version of torpor. Hibernation is longer (several weeks to months) and is typically associated with winter.
echolocation	Production of very high frequency sound (20-200kHz) from the mouth (in some species, the nose) and subsequent listening to echoes of that sound. Microchiropteran bats use echolocation to locate and discern prey objects as well as for navigation. Because it is based entirely on sound waves, echolocation allows bats to "see" in complete darkness (bats also have normal vision).
roosting	The act of resting by a bat. Can occur for short intervals during nighttime foraging, but typically refers to daily resting. Roosting can take place in a variety of places including caves, trees, bridges, or buildings.

Bats use a variety of signals and cues to make decisions. For example, Geoffroy's tailless bats (*Anoura geoffroyi*) used information from both echolocation calls and vision to navigate a maze (Chase 1983), and brown long-eared bats (*Plecotus auritus*) used both visual information and echolocation to locate prey items (Eklöf and Jones 2003). Microchopteran bats choose whether or not to pursue a prey item at least in part based on sounds reflected from echolocation (Simmons and Kick 1983). Female cave myotis bats (*Myotis velifer*) tend to choose maternity roost locations with environmental conditions favorable to pup growth (Buecher and Sidner

1999). Female greater sac-winged bats (*Saccopteryx bilineata*) appear to use both male odor and male 'songs' when deciding on a mate (Voigt and von Helversen 1999; Behr et al. 2006). Little brown bats (*Myotis lucifigus*) choose habitats for foraging which are likely to yield higher foraging success, even if that habitat may be more difficult to navigate due to its complexity (Kalcounis and Brigham 1995).

It seems clear that bats make many decisions regarding many different aspects of the environment using an array of information. Memory retention from previous experiences also likely influences decisions that bats make (Ruczyński and Siemers 2011). Nevertheless, we should expect that in all decisions a bat makes, some pieces of information are more important than others.

Because of their physiology and anatomy (e.g., small mass, high surface-area-to-volume ratio combined with high metabolic rates), conserving energy is crucially important to bats. Bats in temperate areas of the world have a useful tool for coping: the ability to raise and lower the body temperature. Body temperature can approach ambient temperature even in sub-freezing temperatures. Torpor and arousal from torpor thus provides advantages for bats, but it also has downsides (e.g., increased susceptibility to predators).

As night approaches, each individual bat has a decision to make regarding its individual energetic status: should it remain in torpor, arouse from torpor and move to a different roosting location, or should it leave the roost and forage? A bat must consider the energetic costs and benefits of each of these options in order to make a choice that maximizes its relative fitness. Roosting and thermoregulation are integral to bat biology; insights into how bats respond to external conditions are crucial for understanding the evolutionary history and ecology of bats and other mammals as well as for conservation and management decisions.