

Chapter 12

The Ecology of Social Life: A Synthesis

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Abstract All the chapters of this book highlight to some extent the importance of kinship in the evolution of social life throughout the animal kingdom. They also accentuate that variation in genetic relatedness alone is not sufficient to explain the occurrence or details in the organization of social life. A comparative summary of the ecological and demographic factors favoring social life reveals some striking patterns of correlated traits (sociality syndromes). Accordingly, three types of sociality can be distinguished: (i) Aphids, thrips, wood-dwelling termites and the naked mole rat are all groups of totipotent individuals without intensive alloparental care protected by altruistic defenders. They have a long-lasting bonanza-type resource and a safe nest that offers the opportunity of inheriting the natal breeding position. (ii) Social Hymenoptera and non-wood dwelling termites with sterile or subfertile workers are characterized by intensive, altruistic alloparental care that usually involves progressive food provisioning. (iii) Cooperatively breeding vertebrates and social Hymenoptera with totipotent workers (e.g., wasps and queenless ants) take an intermediate position between class (ii) and class (i). Helpers here can gain indirect fitness benefits through alloparental care as well as direct benefits through inheriting the breeding position or by founding an own nest.

12.1 Kin Selection, the Key to the Evolution of Social Life

Cooperation, altruism, and sociality have long been considered as major forces in evolution, albeit the attention they have received relative to that paid to competition, parasitism, and other forms of antagonism has varied over the last 150 years from undue disregard to similarly unjustified preponderance (see Chap. 1).

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Comparable ups and downs have characterized the importance of kin selection as the key explanation for the evolution of altruism. While it needed almost a decade before W.D. Hamilton's inclusive fitness theory (Hamilton 1964) became more widely known, let alone accepted, among biologists (e.g., Hamilton 1996), some 40 years later few researchers doubt its fundamental importance. Though new-group or multilevel selection has repeatedly been spearheaded as seemingly non-kinship-based alternatives for kin-selection theory (Alonso and Schuck-Paim 2002; Wilson and Hölldobler 2005; Wilson 2005), such approaches often appear to suffer from common and long-lasting fallacies (Dawkins 1979; Foster et al. 2006). Consequently, proponents of kin-selection theory have repeatedly emphasized the critical role of kinship in the evolution of altruism (Foster 2006; Foster et al. 2006; see Chap. 1).

As can be told from the chapters in the present book, studying sociality over a wide range of animals strongly supports this view. If helping reduces the helper's direct fitness it is essential that helping is directed towards relatives, because otherwise the 'genes' underlying the helping trait would be propagated less efficiently to the next generation than those of unrelated, selfish individuals, which do not help. New group-selection models ('multilevel selection') therefore do not provide an alternative to kin selection (Hamilton 1975; Queller 1992; Frank 1998; Chap. 1), though, as will be explained in more detail below, they present a promising way of investigating social phenomena. They consider groups as an additional unit of selection with selection simultaneously occurring at different levels, e.g., between individuals in the group and between groups, and the strength of selection depending on the co-variance of genetic traits at the different levels (see also Price 1970; Hamilton 1975; Wilson 1975; Wade 1978a; Sober and Wilson 1997). The predominant factor that increases this covariance, decreases conflict within groups and strengthens selection among groups is the common ancestry of group members. Though other factors, such as green-beard alleles or habitat heterogeneity, may in principle also lead to a positive assortment of altruists (Dawkins 1976; Wilson and Dugatkin 1997; Pepper and Smuts 2002; Axelrod et al. 2004), they appear to be rare in nature (Grafen 2006). Because in nature, the co-variance of genetic traits mostly, if not exclusively, relies on common ancestry, new group selection and kin-selection models become equivalent (Wade 1978b; Grafen 1984; Queller 1992). Both make the same predictions about which conditions favor altruism, but differ in their emphasis on different variables. In kin-selection models, relatedness is the most obvious variable and also the one that can be quantified most easily. Other factors are less explicitly hidden in the cost and benefit terms in Hamilton's famous inequality (Hamilton 1964). In contrast, the new group-selection models accentuate between- versus within-group selection and thus focus on group level phenomena, such as the effects of group size. Kin selection becomes a special form of new group selection specifically applicable for interactions among conspecifics, whereas new group-selection models more generally include also the evolution of cooperative interactions between species, as in symbiosis (e.g., Frank 1997; Wilson 1997).

Kin-selection (and, correspondingly, new group-selection) models similarly are applicable to explain the evolution of cooperation (mutual benefit; sensu Chap. 1), i.e., when interacting partners receive direct benefits from their association that are greater than the resulting costs. In contrast to altruism, there is no loss in direct reproduction. Kinship may nevertheless be important also in this context as it reduces conflict among the interacting partners and aligns their evolutionary interests. Cheating is therefore less likely to evolve. Thus, Hamilton's rule describes both the evolution of cooperation and that of altruism and either direct benefits or indirect benefits ensure that the inequality is fulfilled. Only if the costs of an action are smaller than its benefits (direct in the case of cooperation and indirect in the case of altruism) will it be favored in evolution.

12.2 Common Patterns Among Social Organisms

12.2.1 Importance of Kinship

All chapters of this book emphasize the importance of kinship in the evolution of social life throughout the animal kingdom. The same appears to apply to those social organisms that are not covered in this book, such as social microorganisms (Crespi 2001; West et al. 2006; Foster et al. 2007), ambrosia beetles (Kent and Simpson 1992; Peer and Taborsky 2007) and communal spiders (Whitehouse and Lubin 2005). Cooperation and altruism among conspecific individuals usually occur in kin groups, mainly families, when offspring delay maturity and stay at the natal nest.

At the same time, the chapters accentuate that variation in relatedness alone is not sufficient to explain the occurrence or details in the organization of social life. Given that Hamilton's rule is composed of three variables, this might at first glance appear trivial. Yet, ecological costs and benefits of cooperation have often been disregarded in standard textbooks, e.g., when the evolution of eusociality in social Hymenoptera is erroneously attributed to haplodiploidy alone, or when it is stated that the degree to which altruistic behavior should be extended toward other individuals depends only on the relatedness between helper and recipient. Examples from this book show that variation in relatedness alone is not sufficient to explain the occurrence or pattern of helping behavior in the stenogastrine wasp, *Liostenogaster flavolineata* (see Chap. 4) or the occurrence of 'workers' in the basal termite, *Cryptotermes secundus* (see Chap. 6). Across species of aphids, the occurrence of altruistic soldiers does not correlate with relatedness levels and, although all aphids are clonal, only a few species have soldiers (see Chap. 2). Furthermore, it cannot explain cooperative breeding in some bird species, where helpers aid in raising unrelated young (see Chap. 8). Similarly, variation in the social organization of ants (see Chap. 6) and primates (see Chap. 11) can hardly be explained by relatedness alone. Variation in

relatedness does neither explain variation in worker reproduction among ant species (see Chap. 6; Hammond and Keller 2004; but see Wenseleers and Ratnieks 2006) nor the occurrence of dispersal patterns and composition of groups in primates (see Chap. 11). Whereas kinship can easily be quantified using genetic markers—though its exact meaning and the appropriate level of analysis may occasionally remain obscure to empiricists (Creel 1990; Lucas et al. 1996; Queller 1996)—ecological factors as hidden in the c and b terms of Hamilton's rule are inherently difficult to measure.

12.2.2 *Importance of Ecological Factors*

A comparison of the different chapters reveals a number of ecological factors that repeatedly show up as vital for the evolution of sociality. Previous syntheses have similarly aimed at identifying fundamental ecological and life-history traits (Alexander 1974; Emlen 1982; Stacey and Ligon 1991; Reeve 1998; Johnstone 2000; Whitehouse and Lubin 2005), and consequently some overlap exists between earlier work and our overview in Table 12.1. In the following section, we summarize the factors that appear to be important, and discuss them in the context of previously proposed hypotheses.

Corresponding to the “ecological constraint hypothesis” (Emlen 1982, 1997), three factors favor the offspring's staying at the parental nest: (i) limitation of nesting sites, (ii) high dispersal-related mortality costs, and (iii) demographic factors like group size.

- (i) Limitation of nesting sites has been shown to play a prominent role for the occurrence of helpers in birds (Hatchwell and Komdeur 2000; Dickinson and Hatchwell 2004; Chap. 8) and was also suggested as important for the evolution of polygyny and high reproductive skew in ants (e.g., Bourke and Heinze 1994; Chap. 6). In contrast, providing additional nests did not affect the occurrence of helping behavior in the stenogastrine wasp *L. flavolineata* (Field et al. 1998), which, together with the availability of vacant nests in natural populations, suggests that nest site limitation is less important in the evolution or maintenance of helping in this species.
- (ii) High mortality during dispersal seems to be a common phenomenon in all social organisms, especially thrips, termites, and naked mole-rats. In social Hymenoptera (and several termites), it might have selected for the founding of new societies by reproductives leaving the parental colony with a group of workers in a process called swarming or budding. In microorganisms, the dispersal phase is similarly the stage during which individuals ‘behave socially’ and form groups, and apparently they preferentially aggregate with clonemates (Mehdiabadi et al. 2006). Sociality may also be associated with dispersal in social mammals, albeit to a lesser extent. For example, male lions can form alliances that leave the natal group and have a higher chance of taking over female

Table 12.1 Factors considered important for favoring the evolution of sociality and group living

Genetic	Aphids ¹		Thrips ¹		Bees / Wasps ²		Wasp ^{3,a}		Ants ²		Termites		Birds ³		Mole rats ¹		Mammals ^{1,3}	
	Clonal	Haplo-diploidy	Haplo-diploidy	Haplo-diploidy	Haplo-diploidy	Haplo-diploidy	Haplo-diploidy	Haplo-diploidy	Haplo-diploidy	Haplo-diploidy	OP: MP ²	Diploid	Diploid	Diploid	Diploid	Diploid	Diploid	Diploid
Habitat saturation	-	-	-	-	-	-	-	-	+	polygyny	-	+	+	+	-	-	-	-/+
Dispersal costs	-	+	-	-	-	-	-	-	+	+	OP: + MP: +	+	+	+	+	+	-/+	
Demography	+	+	-	-	-	-	-	-	+	+	+	+	+	+	+	+	-	
Foraging/Allofeeding ^b	-	-	+	+	+	+	+	+	+	+	OP: - MP: +	+	+	+	-	-	limited due to lactation	
Bonanza type resource	+	+	-	-	-	-	-	-	-	-	OP: + MP: -	-	-	-	+	+	-	
Fortress ^c defense	+	+	-	-	-	-	-	-	-	-	OP: + MP: -	-	-	-	+	+	-/+	
Predator/parasite defense ^d	+	+	+	+	+	+	+	+	+	+	OP: - MP: +	-	-	+	+	+	+	
Inbreeding	+	+	-	-	-	-	-	-	-	-	OP: + MP: -(+)	-	-	+	+	+	-	
Inheritance ^f	+	+	- (+)	-	+	+	+	+	- ^e	- ^e	OP: + MP: -(+)	+	+	+	+	+	-/+	
Nepotism ^g	-	+	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	

Three sociality syndromes can be identified, which are marked by different indices: type (i)¹; (ii)²; (iii)³. Type (i) species are characterized by a bonanza-type food resource, fortress defense, inheritance opportunities, and the possibility of inbreeding, while allofeeding is of low importance. Type (ii) species are characterized by allofeeding and absence of a bonanza-type resource and fortress defense with inbreeding avoidance and generally few opportunities to inherit the natal breeding position. Type (iii) species have an intermediate position with allofeeding being important, but having the opportunity to inherit the natal breeding position, although this might be limited by the necessity to avoid inbreeding. Cooperatively breeding mammals have species that belong to type (i), while others belong to type (iii). +: important factor; -: factor with low importance (for inbreeding: - indicates strict inbreeding avoidance); OP: wood-dwelling, one-piece nester termites; MP: non-wood-dwelling, multiple-pieces nester termites.

^aMainly based on results for *Liostenogaster flavolineata*

^bForaging and allofeeding offer the opportunity for load lightening of the breeders; local resource competition is prevented by increasing the food intake

^cDefense is mainly directed against competitors that try to invade/occupy the nest

^dDefense is mainly directed against predators and parasites

^eExcept for species with gamergates where nest inheritance is common

^fIndividuals can regularly gain direct fitness in the nest by inheriting the breeding position

^gNepotism, not true kin discrimination, sensu Grafen (1990)

prides than solitary males (Heinsohn and Packer 1995). In wild dogs, spotted hyenas, and primates, large groups can split to subsequently occupy two territories (Solomon and French 1997). Even after dispersal, the small chance that an individual will survive long enough to rear offspring through maturity favors helping over independent reproduction in primitively eusocial wasps (Gadagkar 1991; Queller and Strassmann 1998; Field et al. 2000; see Chap. 4).

- (iii) Finally, demography, i.e., population density, has been shown to explain some variability in the degree of altruism. As predicted by a model, thrips and aphids produce more soldiers when their density in the gall is high and birth rate is low (see Chaps. 2 and 3). In such situations, the costs of producing a soldier compared to a sexual are low because groups exist at their carrying capacity. In the stenogastrine wasp *L. flavolineata* and the termite *C. secundus* colony size influences the degree of altruism and cooperation, respectively. Termites are more likely to develop into dispersing sexuals when colony size is high and hence the probability to inherit the colony is low (see Chap. 7). Wasps work less hard if they are high up in the colony's dominance hierarchy and so have a good chance of becoming a reproductive in the future, and if the group they might to inherit is larger (Field et al. 2006). The position in the queue similarly influences the amount of alloparental care provided in several birds (Koenig and Dickinson 2004). The influence of demographic factors in ants, bees, and mammals is less clear, but Tsuji (2006) has recently demonstrated the importance of population density and growth rate for the evolution of colony characteristics, such as queen number, in ants.

Corresponding to the "benefits of philopatry hypothesis" (Stacey and Ligon 1991), four factors favor sociality through individuals gaining inclusive fitness at their natal nests: indirect fitness through (i) alloparental brood care and (ii) defense of relatives against parasites and predators; (iii) direct fitness through nest inheritance or increased experience; and (iv) both, direct and indirect fitness, through the monopolization of a "bonanza-like" food source against competitors.

- (i) Indirect fitness benefits through alloparental brood care appear to be particularly important in social Hymenoptera, higher termites, and several birds. In mammals, the ability to care directly for the offspring of others is often restricted by the need of having lactating females (Solomon and French 1997). Thus, non-reproducing helpers in mammals can only gain indirect fitness benefits when providing food for the parents increases their respective reproductive success or when they play an important role in provisioning young after weaning. Hence, the potential to provide care, the potential to increase the reproductive success of the breeder by helping and load lightening, and progressive food provisioning are facilitators of alloparental brood care. The rarity of sociality in sphecoid wasps compared to bees might thus be explained by their inability to provide help because of a different type of food provisioning (see Chap. 5). The type of food is similarly essential for the occurrence of altruistic helping in termites. In wood-dwelling termites, like *C. secundus*, the potential to reduce the workload of reproductives is small, as all individuals live within their food and extensive,

costly foraging is not necessary (Korb 2007). In species in which nest and food are separated, individuals can considerably help the reproductives by providing the young with food that is costly to collect. A similar association between load lightening and helping is also found in birds (Heinsohn 2004).

- (ii) Indirect fitness can also be gained by efficiently defending relatives against predators and parasites. This seems to play a role in several cooperatively breeding mammals where non-reproducing offspring stay at the nest as ‘guards’ that warn young by alarm calls, as in the case of Belding’s ground squirrel (Sherman 1977) (although it is questionable whether these calls are always altruistic, i.e., associated with costs to the caller; for meerkats it has been shown that they confer direct fitness benefits; Clutton-Brock et al. 1999). Defense seems to be less important in most cooperatively breeding birds, although several exceptions may exist. For example, alarm calls are a common phenomenon in Arabian babblers (Zahavi 1990). In insects, predators (and especially parasites) constitute an important selection pressure although it strongly depends on the type of parasite whether group living can offer protection (see Chap. 5). In social Hymenoptera, parasitism has been invoked to explain variation in the structure of societies, in particular mating frequency. According to the “diversity against parasites hypothesis”, genetically more diverse colonies are better protected against parasites and pathogens (Sherman et al. 1988; Baer and Schmid-Hempel 1999; Brown and Schmid-Hempel 2003). In ants, polygyny seems to offer better protection against social parasites, such as slave-making ants, due to larger colony sizes and a higher chance that one queen survives a slave-raid (see Chap. 6). In contrast, social life in aphids, thrips, termites, the stenogastrine wasp *L. flavolineata* and naked mole rats, in general, seems to provide protection more against intraspecific competitors than predators or parasites (see below; Cronin and Field 2007).
- (iii) Direct fitness gains through nest inheritance can potentially play an important role in species with totipotent helpers / workers, such as those social Hymenoptera, where workers can mate and produce both female and male offspring, wood-dwelling termites, aphids, and thrips in which soldiers can still reproduce, the naked mole-rat and cooperatively breeding vertebrates. In social Hymenoptera, such as monogynous ants, which build large colonies, nest inheritance plays a minor role, probably because the chance of inheritance is zero or negligible, and because parasites and pathogens accumulate in their nests. Additionally, in analogy to Metazoa that undergo a single-cell stage during embryogenesis, a single-queen founding phase might punish selfish genetic lineages (Heinze et al. 2001). Direct benefits arising from individuals acquiring skills in brood care, which later increase their own breeding success, seem restricted to some cooperatively breeding vertebrates with more complex behavior of brood care and brood provisioning (Komdeur 1996; Russell 2004).

Incest avoidance often prevents inheriting the breeding position in cooperatively breeding birds and mammals, and the necessity to outbreed creates complicated dynamics in vertebrate groups and results in a high fluctuation of

group members (Pusey and Wolf 1996; Emlen 1997; Koenig and Haydock 2004). Either the heir to the nest must be an alien or an offspring must find an unrelated mate. In contrast to social Hymenoptera, where inheriting queens are supposed to avoid inbreeding by mating with alien males (e.g., Hölldobler and Bartz 1985), considerable conflicts arise in social vertebrates and often lead to the breakdown of groups (Emlen 1997). In social Hymenoptera, alien males play only a transient role as they die shortly after mating (Boomsma et al. 2005). In social vertebrates, alien breeders remain in the group together with unrelated older offspring, with whom they compete for access to food etc. The resulting conflicts lead to the dispersal of unrelated older offspring or, in extreme cases, infanticide, as in lions and Hanuman langurs (Hrady 1977; Pusey and Packer 1994), and certainly limit the benefits of nest inheritance. In termites, inbreeding seems to be less of a problem. Strikingly, the only social mammal with castes, the naked mole rat, shows considerable degrees of inbreeding (see Chap. 10). Although the benefits from nest inheritance have rarely been measured, they are probably very important factors for the evolution of sociality in the naked mole rat, social wasps and a few species of ants, where totipotent workers can inherit the natal breeding position when the current breeder dies. For the wood-dwelling termite *C. secundus* (Korb 2007) as well as some bird species, such as the Australian Magpie (Veltman 1989), where individuals stay at the nest and do not work, or for those birds where helpers raise unrelated offspring (Reyer et al. 1986; Dunn et al. 1995), staying for direct benefits apparently is the driving force of social life.

- (iv) Both direct and indirect benefits, which accrue to individuals through monopolization of a “bonanza-like” type of food, seem to be crucial for the evolution of social life in aphids, thrips, wood-dwelling termites and the naked mole rat. These species, together with spiders (Whitehouse and Lubin 2005) have in common that their nest is identical (aphids, thrips, wood-dwelling termites) or closely linked (naked mole rat, social spiders) with their food. This allows individuals to coexist over long periods without local resource competition and favors group-living in that the resource can be defended against competitors. Consequently, soldiers have evolved in most of these taxa, which defend the resource against competitors rather than the group against predators and parasites. Similar, but to a lesser extent, increased foraging efficiency and monopolization of resources also seem to favor group-living in some primates (see Chap. 11) and carnivores, such as wolves, wild dogs, foxes, and spotted hyenas (Gittleman 1989; Creel and Creel 1995).

12.3 Sociality Syndromes

A comparative summary of the ecological factors favoring social life reveals some striking patterns of correlated traits (Table 1). Accordingly, three types of sociality can be distinguished, each with a unique combination of ecological factors:

- (i) Aphids, thrips, wood-dwelling termites and the naked mole rat are all groups of totipotent individuals protected by altruistic defenders or soldiers. They monopolize a long-lasting bonanza-type resource, which supports the co-existence of many individuals without selection for dispersal (Hamilton and May 1977). The totipotent individuals do not provide intensive alloparental care, probably because food is easily accessible to all individuals and alloparental care cannot strongly alleviate the reproductive burden of breeders. Helpers seem to stay because the nest is a safe haven with plenty of food and a substantial possibility of inheriting the natal breeding position. The chances of founding an own nest independently are low due to high mortality risks during dispersal in an unfavorable environment. The only truly altruistic individuals in these groups are the defenders (soldiers), which mainly protect the resource against competitors and partly against predators. According to Queller and Strassmann (1998), such altruistic individuals can be called “fortress defenders”. Inbreeding, which regularly occurs in such societies, seems to play an important role, not necessarily through increasing relatedness, but through reducing relatedness asymmetries in the haplodiploid thrips (see Chap. 3) and stabilizing groups over longer periods as heirs do not have to mate with unrelated, alien partners (in contrast to vertebrates).
- (ii) Social Hymenoptera and non-wood dwelling termites with sterile or subfertile workers are characterized by intensive, altruistic alloparental care. They engage in costly helping with low chances of reproducing. Brood care usually involves progressive food provisioning, which is costly to the reproductives and can be ‘handed over’ to workers. Consequently, reproductives can concentrate on egg laying.
- (iii) Cooperatively breeding vertebrates and social Hymenoptera with totipotent workers (e.g., wasps and queenless ants) take an intermediate position between societies with altruistic, subfertile workers of class (ii) and those consisting of the totipotent individuals of class (i). Helpers can gain indirect fitness benefits through alloparental care as well as direct benefits through inheriting the breeding position or, in many cases, by founding an own nest. In vertebrates, group instability due to inbreeding avoidance, together with other factors such as their comparatively low fecundity, might be one explanation for the lack of large social vertebrate groups (with the exception of naked mole rats which show inbreeding; see Chap. 10). The ecological factors favoring alloparental care in totipotent workers are identical to those for subfertile workers of class (ii), namely the potential to provide costly help that frees the reproductives from provisioning their offspring. At the same time, one would expect that totipotent individuals are less altruistic or adjust their altruistic investment according to their chances to inherit the breeding position (Kokko and Johnstone 1999). Although not many data exist, those available suggest that they indeed do: depending, for instance, on their own rank in the society’s hierarchy, wasps and birds invest differentially in alloparental care (Field et al. 1999; Koenig and Dickinson 2004; Cant and Field 2005). Additionally, at least in some birds, totipotent workers seem to adjust

their helping behavior to dispersal opportunities: when provided with extra nesting sites, helpers in the Seychelles warbler left the natal nest (Komdeur 1992; Komdeur et al. 1995). The comparatively small group sizes of coexisting totipotent workers might be explained by several factors: (i) The opportunity of founding independently, (ii) presumed decreasing benefit of helping with increasing group size (Michener 1964; Reyer 1984; Karsai and Wenzel 1998) and (iii) the limitation of food sources, which causes local resource competition. In queenless ants, where totipotent gamergates presumably are not capable of founding independently, group sizes are often much larger, which indicates that limited dispersal options force helpers to stay and leads to larger group size.

12.4 Future Perspectives

As this book demonstrates, social evolution is driven by a number of different ecological conditions, and three particularly important classes of selection pressures seem to emerge (Table 12.2). The knowledge of the ecological forces differs strongly between different types of animal societies as has especially been shown for social vertebrates. For social insects, clearly more ecological studies are needed to determine their importance (Boomsma and Franks 2006). The impact of ecological factors is hidden in the cost-and-benefit terms of Hamilton's rule, which makes an easy quantification difficult. Applying a multilevel selection approach might therefore be fruitful. As mentioned above, it is equivalent to the kin-selection approach, but because it more clearly stresses parameters, such as group size, it might thus be helpful to obtain a more complete understanding of social phenomena (Foster 2006). While kinship has often been considered the most obvious and prominent parameter in Hamilton's rule, multilevel selection also concentrates on the individual versus the group component of fitness. The latter is certainly of fundamental importance in social insects, because properties emerging through the interaction of individuals, such as thermoregulation, social homeostasis, and ecological dominance, are selected on the level of the "superorganismic" colony (Korb and Heinze 2004). Selection on colonies increases colony efficiency, partly at the cost of the interests of single individuals. Thus, the lack of true kin discrimination in social Hymenoptera or the widespread absence of worker reproduction is explained by the negative effect they would have on colony-level efficiency (Ratnieks 1988; Hammond and Keller 2004). However, our knowledge of the effects of group size or unpoliced worker egg laying on the overall reproductive success of a colony is surprisingly limited (but see Hartmann et al. 2003). Taking such group-level effects into account will certainly help to resolve apparent mismatches between predictions from kinship relations and the behavioral decisions of individual group members.

Table 12.2 Characterization of the three sociality syndromes

	Type I	Type III	Type II
Characteristic traits	<ul style="list-style-type: none"> • Bonanza-type food • Fortress defense • Inheritance opportunities • Inbreeding possible • No allofeeding 	<ul style="list-style-type: none"> • No bonanza-type food • No fortress defense • Inheritance opportunities • Inbreeding limited • Allofeeding -> load lightening 	<ul style="list-style-type: none"> • No bonanza-type food • No fortress defense • Few/no opportunities for inheritance • Allofeeding -> load lightening
“Castes”	Less altruistic immatures + Soldiers	Helpers	Workers
Driving Factors	<ul style="list-style-type: none"> • Mainly direct fitness for most individuals, except few soldiers 	<ul style="list-style-type: none"> • Direct + indirect fitness 	<ul style="list-style-type: none"> • Mainly indirect fitness
Taxa	<ul style="list-style-type: none"> • Aphids • Thrips • Wood-dwelling termites • Naked mole-rat 	<ul style="list-style-type: none"> • Most wasps • Cooperatively breeding birds • Some cooperatively breeding mammals 	<ul style="list-style-type: none"> • Ants (except species with gamergates) • Most bees • Non-wood-dwelling termites
Evolutionary transitions	<p>Wood-dwelling termites</p> <p>Naked mole-rat</p>	<p>Wasps</p> <p>Ants</p>	<p>Non-wood-dwelling termites</p> <p>Some cooperatively breeding mammals</p>

Shown are the characterizing traits, the evolved “Castes”, the driving evolutionary forces, the distribution of the three sociality types among taxa and likely evolutionary transitions between syndromes

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