

# 1 Introduction

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Why is the evolution of social behaviour interesting? For one thing, if we wish to comprehend the origin, maintenance and functionality of any biological trait, we need to understand its *evolution*. At the same time, each behaviour is *social* in essence; it affects the survival, production and reproduction of others in some way or another. ‘Others’ encompasses social partners including mates, offspring, competitors, friends and foes regardless.

But what is it that brings animals together? Why are individuals attracted by others, interact with them or form groups? What explains the staggering diversity of animal social systems? To start to address these questions it seems useful to distinguish between ecological causes and the functions of social behaviour. For instance, it may be safer to be in a group because of high predation pressure, which represents an ecological cause for social contact, or it may be beneficial to aggregate to choose a mating partner, which is a functional reason for social attraction. Obviously, ecological causes and social functions can be intertwined. In any case, living together entails competition for resources and involves different types of interactions between conspecific contenders, which show different functional characteristics and fulfil different roles (Wilson 1975).

A conspicuous attribute of social units that immediately catches one’s eye is the size of a group. Clearly, the smallest social unit is a group of two or a ‘dyad’, whereas there is no defined upper limit to group size, if we imagine vast fish schools, ant colonies or herds of wildebeest. But not only is the number of partners important for the evolution of adaptive responses to the challenges involved in social interactions, the relationship between partners and the dynamics of group membership are also essential. At one end of the spectrum, groups may form in which there is little or no relationship between members; for instance, aggregations may just reflect the distribution of resources. At the other end of the spectrum, groups may consist of particular individuals that are not exchangeable because they fulfil certain roles that are complementary, or are characterized by individual (personalized) relationships among group members. Hence social units can be characterized both by group size and composition and by their membership dynamics.

*Dyads* refer to interactions between two players, corresponding to the most basic units of sociality. Dyadic interactions may be short-term, such as when an intruder confronts a territory owner or when a male and a female mate in a promiscuous mating system. In contrast, they may last for extended periods, perhaps an entire lifetime,

such as when sibling partners share resources and mates (Maynard Smith & Ridpath 1972; Foster 1977, 1981; Packer & Pusey 1982; Packer et al. 1991; Krakauer 2005; Krakauer & DuVal 2011), and in permanent monogamous pairs (Klug 2018; Kvarnemo 2018). As dyads constitute the simplest social structure, most theoretical models dealing with behavioural decisions in competitive situations have focused on this interaction unit (Kokko 2013). Well-known examples include the game-theoretical treatments of pair-wise contests (Maynard-Smith 1982a), whether in singular (e.g. one-shot games; Rand et al. 2013) or repeated interactions (e.g. iterated prisoner's dilemma games; Axelrod & Hamilton 1981). Experiments using dyads to study social decisions are also abundant due to the methodical manageability and clear predictability of behaviour (Hsu et al. 2006; Arnott & Elwood 2009; Lehner et al. 2011; Green & Patek 2018; Schweinfurth & Taborsky 2018a, 2018b).

*Multi-member open groups* denote assemblies of individuals characterized by dynamic membership and are often rather temporary. Examples include foraging and mating aggregations, migratory groups, schools, shoals, swarms and flocks. The functional causes of such aggregations may be the underlying distribution of used resources (Bentley et al. 2001; Bos et al. 2004; Masse & Cote 2013; Halliwell et al. 2017), reproduction (Domeier & Colin 1997; Campbell et al. 2008), the reduction of predation risk (Foster & Treherne 1981; Pitcher 1986; van der Marel et al. 2019), or the use of public information either to find resources (Coolen et al. 2003; Canonge et al. 2011; Laidre 2013; Bijleveld et al. 2015) or to increase safety (Thünken et al. 2014a; Mehlis et al. 2015).

*Multi-member closed groups* are characterized by more or less stable membership. Such groups may be rather unstructured, like certain aggregations that remain localized but lack specific relationships (such as dominance) among group members (e.g. long-term, localized, non-reproductive aggregations in cichlid fish; Taborsky & Limberger 1981). Alternatively, closed groups with little immigration, if any, may be characterized by individualized relations and a clear structure. In most cases, the functional background of such groups is reproduction, and their specific organization is determined by relatedness, dominance and sex of group members. The simplest and most widespread social units of this type are families with one or both parents caring for their offspring, which often coincides with resource monopolization (Clutton-Brock 1991). Sometimes, such groups persist beyond the completion of brood care, which may coincide with cooperative care of subsequent offspring by parents and young of previous broods (Skutch 1961; Taborsky 1994; Cockburn 1998; Koenig & Dickinson 2016). Alternatively, several group members may reproduce more or less independently and raise their offspring jointly (Eisenberg et al. 1972; Kappeler & van Schaik 2002; Riehl 2011, 2013). The most advanced closed multi-member groups exhibit various levels of task sharing among their members (Lacey & Sherman 1991; Bruintjes & Taborsky 2011; Holbrook et al. 2011; Pruitt & Riechert 2011; Parmentier et al. 2015), which culminates in the lifelong division between reproduction and labour by different castes (Hölldobler & Wilson 1990, 2009; Benton & Foster 1992; Crespi 1992; Thorne 1997; Bornbusch et al. 2018).

So it seems there are numerous reasons why animals get together and form groups of various sizes, compositions and membership dynamics. On the face of it, sociality seems to offer distinct advantages over solitary life, but we need to remember that organisms live in a world of competition. Behind every thicket, over and under every surface, from microbes to humans: individuals compete. And not just individuals; cultures compete, economies compete, ideas compete. Nature is red in tooth and claw in endless variations. Charles Darwin (1859) conceptualized competition for resources as the motive force in the evolution of life. Even in a land of plenty, organisms will reproduce at maximum output until they find themselves in a situation of resource limitation. The ineluctable nature of competition is one of the basic elements of ecology and a major theme in evolutionary research (Begon et al. 2006).

## 1.1 A Historical Perspective

How individuals of the same species compete for food, shelter, mates and other resources required for survival and reproduction is among the most obvious and enthralling observations to be made in nature. Conspecifics typically have exactly the same requirements, hence they are each other's greatest competitors. For this reason we cannot easily explain cases where individuals forgo benefits that would otherwise raise their own fitness in order to support conspecifics, that is, to accept costs for the benefit of others. This problem – explaining the evolution of cooperation and altruism – is thus one important focus of this book.

Darwin recognized that cooperative behaviour for the good of others was a critical challenge to his theory of evolution. In *On the Origin of Species*, he writes that 'Natural Selection will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each' (Darwin 1859). Consequently, observations of apparent altruism, where individuals accept to pay a cost for the benefit of somebody else, represented a fundamental problem for Darwin's theory, as he was the first to point out: 'I will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect-communities . . . this is by far the most serious special difficulty, which my theory has encountered'. This 'special difficulty' of altruistic behaviour, the sacrifice of own fitness for the sole benefit of someone else, has intrigued evolutionary biologists ever since. After all, 'altruism is the very opposite to the survival of the fittest' (Sober & Wilson 1998, p. 19), causing the progenitor of 'sociobiology', Edward O. Wilson, to call it 'the central theoretical problem of sociobiology' (Wilson 1975, p. 3). Some ethologists thought they had solved the problem by assuming that individuals act not for their own benefit but for the good of the species (Lorenz 1963). Similar ideas thrived in ecology (Wynne-Edwards 1962), when William Hamilton worked out a formal solution to the problem of altruism, which was at the same time both logically rigorous and remarkably intuitive: the idea that natural selection acts on inclusive fitness, not just personal fitness (Hamilton 1963, 1964). Hamilton's theory transformed evolutionary thinking

by highlighting the importance of relatedness between the altruist and the recipient of a helpful act. This seemingly simple but essential insight revolutionized behavioural and evolutionary biology (Williams 1966; West-Eberhard 1975; Wilson 1975; Dawkins 1976; Brown 1983). Suddenly, the altruistic help of close kin was understood as an inherent component of an individual's Darwinian fitness, removing much of the mystery from the problem that had troubled Darwin more than a century before.

The advent of kin selection theory did not solve all problems encountered in the context of cooperation and altruism (see Box 1.1 for definitions). Kin selection cannot explain many aspects of cooperation occurring among relatives and, in addition, behaviour causing costs to an actor at the benefit of a recipient is not limited to social interactions between relatives. This observation led evolutionary biologists to search for alternative explanations of altruism in nature. Robert Trivers (1971) proposed that if an individual helps another one this could be paid back in the future, thereby initiating reciprocal altruism. Numerous formal models have attempted to show that the adoption of the simple decision rule 'help an individual that has helped you before' can establish evolutionarily stable levels of cooperation in a population ('direct reciprocity'; Axelrod & Hamilton 1981; Killingback & Doebeli 2002; Andre 2015). Both simpler and more sophisticated decision rules have also been proposed and formally checked for their potential to generate evolutionarily stable levels of cooperation in a population. The simplest such rule, 'help anyone if helped by someone', involves few cognitive demands ('generalized reciprocity'; Boyd & Richerson 1989; Pfeiffer et al. 2005; Rankin & Taborsky 2009; Barta et al. 2011), whereas a rule demanding higher cognitive abilities is 'help someone who has helped someone else' ('indirect reciprocity'; Alexander 1974; Nowak & Sigmund 1998; Milinski 2016). All these decision rules have been shown to create evolutionarily stable levels of cooperation by various modelling approaches, but the cognitive demands for these mechanisms are obviously very different, which may influence their prevalence in nature (Stevens et al. 2005; Schweinfurth & Call 2019a).

We should stress at this point that if actions are beneficial to an actor and at the same time benefit others, these positive by-effects do not need sophisticated evolutionary explanations. The inherent property of such mutualisms is that an action is positively selected by the direct fitness benefits to the actor, which implies that effects to other beneficiaries do not need to feed back to the actor's fitness. What may look like an act of altruistic cooperation is indeed an outcome of the pursuit of self-interests, just like Darwin had claimed (Dugatkin 1997; Taborsky et al. 2016). Such forms of mutualistic cooperation are known from both intraspecific and interspecific interactions (Frank 1994; Clutton-Brock 2009), but they are much more conspicuous – and hence better known – if different species are involved. Also, we should acknowledge that many forms of cooperation do not involve higher costs than benefits to an actor, either concerning immediate fitness effects or long-term fitness consequences. Cooperative acts may even 'produce' resources due to synergistic effects (Comins & Szathmari 2015), for instance when interacting agents benefit from division of labour. Therefore,

the social dilemmas getting most attention in evolutionary theory might be less widespread and important than the impression this extraordinary focus may convey.

Last but not least, behavioural and evolutionary biologists have realized that altruism can be forced by a receiver against the fitness interests of the actor. The raiding of other ants' nests by slave-making ants to recruit workers in order to raise their broods is a vivid case in point (Brandt et al. 2005). Other extreme cases of such forced 'cooperation' or altruism, in the form of interspecific social parasitism, include the raising of broods by the hosts of brood parasites (Davies & Brooke 1989a; Davies 2000). There are many examples of exploitation of the behaviour of one party by another (Barnard 1984) and they are particularly conspicuous if different species are involved (Feeney et al. 2014; Soler 2014; Suhonen et al. 2019). Nevertheless, similar cases of brood parasitism occur within species (Andersson 1984; Petrie & Moller 1991; Field 1992; Zink 2000; Tallamy 2005). Often, individuals exploiting the effort of others against the latter's interest act surreptitiously and succeed if they remain undetected. Alternatively, animals may punish conspecifics that do not deliver the goods and services they demand (Boyd & Richerson 1992; Clutton-Brock & Parker 1995), which may simply reflect a credible threat to desert the interaction (McNamara & Houston 2002). Credible threats can induce cooperative behaviour, especially if alternative options for the social partner are poor (Cant & Johnstone 2009; Cant 2011; Hellmann & Hamilton 2018).

Despite these various alternative explanations of cooperation, the kin selection hypothesis is currently the predominant concept used to explain cooperation among conspecifics (Gadagkar 1997; West et al. 2007c; Bourke 2011; Green et al. 2016). This may be partly because many social interactions, and thus also many acts of cooperation, occur among kin, as in natural populations dispersal tends to be limited and hence interaction partners share genes by common descent (Lehmann & Rousset 2010; Koenig & Dickinson 2016). Moreover, cooperative behaviour seems to be common especially if social and mating patterns result in regular interactions between close kin (Boomsma 2007; Hughes et al. 2008; Cornwallis et al. 2010; Lukas & Clutton-Brock 2012). This does not mean, however, that altruism cannot evolve when relatedness is low (Refardt et al. 2013; Riehl 2013; Quinones et al. 2016; Taborsky et al. 2016). Furthermore, it also does not mean that direct fitness benefits are unimportant when closely related individuals interact with each other (Queller 1985; Frank 1998; Richardson et al. 2002; Griffin & West 2003; Jungwirth & Taborsky 2015). Competition between kin can outweigh the indirect fitness benefits of helping kin (Taylor 1992; Wilson et al. 1992; Queller 1994a; West et al. 2002; Platt & Bever 2009), and examples from several taxa show that kinship can even enhance aggression between group members or adversely affect cooperation propensity among social partners ('negative kin discrimination'; Zöttl et al. 2013a; Dunn et al. 2014; Thompson et al. 2017a; Schweinfurth & Taborsky 2018a). Hence, the widespread tendency to assume that kin selection explains cooperation between relatives seems detrimental to a comprehensive understanding of the evolution of cooperation. Throughout this book, we argue that there is much to learn from a genuine attempt to understand indirect *and* direct fitness effects of behaviour, irrespective of whether it is observed between related or unrelated individuals, and we extend our view across species borders also.

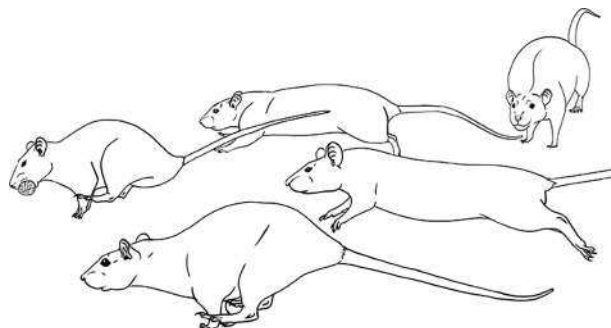
## 1.2 Dealing with Competition

What can individuals do in the struggle for resources that everyone needs? There are three principal tactics to cope with competition for resources: *race* for them (i.e. be there quicker), *fight* for them (i.e. try to monopolize), or *share* them (i.e. concede a quota to competitors). Accordingly, these alternative ways to cope with social competition are a recurring theme in this book. Clearly, there are points of intersection between these solutions. For instance, ‘race’ and ‘fight’ are not necessarily mutually exclusive tactics but may co-occur. When individuals scramble to obtain resources from patches that vary in quality, which can result in an ‘ideal free distribution’ (Fretwell & Lucas 1970) among the competitors, more capable individuals can gain from attempting to hold off competitors from the most profitable patches. In these circumstances, a mixture of ‘race’ and ‘fight’ can ensue, causing an ‘ideal despotic distribution’ (Fretwell 1972; reviewed in Tregenza 1995).

The type of resources competed for has a strong influence on social interactions, which may in turn affect social structure. Even if competition among social partners is often not confined to one type of resource, to deal with different needs separately may illustrate general principles of how to cope best with resource competition. In the following, we shall outline how different needs and functional contexts of resource competition may select for one or the other behavioural tactic; that is, whether it is best to be quick in obtaining a resource (*race*), to monopolize it (*fight*), or to concede some of it to others (*share*).

### 1.2.1 Competition for Food

Competition for food alone (i.e. when not competing for other resources concomitantly) may cause individuals either to *race* or to *share*, but perhaps more rarely to *fight*, as food is often a sharable resource. Hence, if individuals compete mainly for food, we would predict them either to avoid each other or to combine efforts in order to benefit from synergistic effects (e.g. by being more efficient or facing lower risk when hunting or foraging in a group; Packer & Ruttan 1988; Krause & Ruxton 2002; Corning & Szathmary 2015). Importantly, cooperation may even produce public goods and thereby reduce competition (Platt & Bever 2009). Sometimes, food may be economically defensible by individuals or groups, which then can select for monopolization (i.e. *fight*: Dill 1978; Kotschal et al. 1993).<sup>1</sup>



<sup>1</sup> All sketches of Norway rats were drawn by Michelle Gyga.

(a) Race

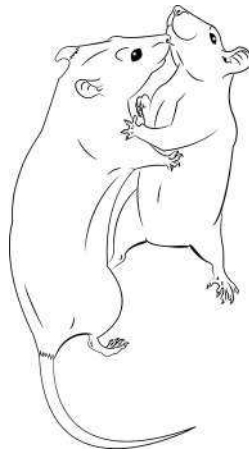
Individuals often aggregate to find food (Valone 1989; Templeton & Giraldeau 1995; Krause & Ruxton 2002). This is particularly common when food is hard to find or unpredictable. Another precondition is that food cannot be economically monopolized (Brown 1964; Maher & Lott 2000; Sorato et al. 2015). In such conditions, individuals benefit from joining others because of the increased chances to find the required resources according to the German and Dutch proverb ‘four eyes see more than two’. Such aggregations of food-seeking individuals, which may also contain individuals from different species (Farine et al. 2012; Sridhar et al. 2012), create a paradoxical situation, because now the competitors for a resource do not space out, but instead connect to each other. Fighting over these desired resources does not pay, however, if they cannot be defended economically. If the food is plentiful locally or temporally, i.e. sufficient to satisfy everyone’s need, there is no inter-individual conflict. Typical examples include mixed herds of grazers (Lucherini & Birochio 1997; Owen-Smith et al. 2015) and shoals/schools of fish (Baird et al. 1991; Foster et al. 2001; Hintz & Lonzarich 2018). If there is limitation, however, it is important to be quicker than others, i.e. to race (Recer et al. 1987; Shaw et al. 1995), which may come at the cost of impaired accuracy in foraging decisions. In zebra finches racing for feed, for instance, faster individuals are more likely to overlook food items (David et al. 2014). The use of a racing tactic in competitive situations has been demonstrated, for instance, in flocks of waders (Beauchamp 2012) and groups of folivorous primates (Teichroeb & Sicotte 2018), and its occurrence was experimentally shown to increase with group size in songbirds (Rieucou & Giraldeau 2009). Scramble may also lead to innovative food acquisition tactics, which can increase feeding efficiency (Morand-Ferron & Quinn 2011).



(b) Share

When several individuals obtain food that is sharable, each of them may do best by sharing with others instead of fighting over it (Elgar 1986; Caine et al. 1995), irrespective of whether the acquisition of the desired resource is incidental or resulting from shared effort. The important precondition for this type of social response is that the benefit of sharing is greater than the alternative possibility of trying to monopolize it by fighting (Dugatkin 1997). The typical food supply

selecting for this type of response is ephemeral or bonanza resources (Heinrich 1988; McInnes et al. 2017), or resources that can be better obtained by group efforts (e.g. by cooperative hunting; Packer & Ruttan 1988; Herbert-Read et al. 2016; Dumke et al. 2018).



(c) Fight

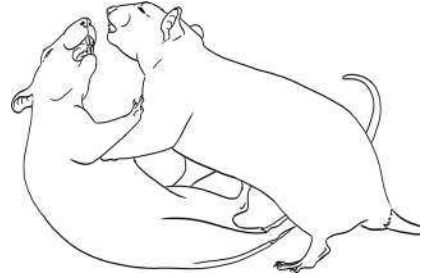
When food can be economically defended (Brown 1964; Rousseu et al. 2014; Sharpe & Aviles 2016) or the renewal rate of a local food source is high enough (Waser 1981; Houston et al. 1985), it may be beneficial to defend either the food itself or an area large enough to sustain the defender. This is exemplified by feeding territories in nectar-feeding birds (Gill & Wolf 1975) and algae-feeding fish (Robertson 1984; Barlow 1993; Kotrschal & Taborsky 2010), or aquatic insects and juvenile salmonids that defend their feeding stations while feeding mainly on drift food (Dill et al. 1981; Hart 1987; Gunnarsson & Steingrimsson 2011; Nicola et al. 2016). Food may be economically defended especially at intermediate abundance, when it pays best according to the threshold model of feeding territoriality (Carpenter & Macmillen 1976; Wilcox & Ruckdeschel 1982; Carpenter 1987; Grant et al. 2002; Toobaie & Grant 2013).

### 1.2.2 Competition for Shelter

If individuals compete for shelter, one might expect them to either *fight* or *share*, because shelters can either be monopolized or shared, but they are typically needed for extended periods of time, so being there first (i.e. to *race*) bears little benefit. Nevertheless, there may be an element of scramble when individuals compete for resources that can be monopolized, because of the common convention ‘owner wins’. Those occupying a territory first thereby may benefit from this somewhat ‘uncorrelated asymmetry’ (i.e. an asymmetry not related to their actual resource holding



potential, or RHP; Maynard Smith 1974; Parker 1974; Hammerstein 1981; Hammerstein & Parker 1982).



(a) Fight

If shelters are limited but important for survival and/or reproduction, and sharing is physically impossible (e.g. due to limited den size), risky (e.g. due to increased exposure to threats), or otherwise costly (e.g. parasite transmission at close contact with conspecifics), they should be defended. This is particularly true in cases where shelters are individually produced and therefore costly, like in many plant-dwelling arthropods (Lill & Marquis 2007; LoPresti & Morse 2013; Cornelissen et al. 2016), fossorial mammals (Nevo 1979; Lacey et al. 1998) and aquatic larvae (Hershey 1987), or where shelter use is vital, such as in hermit crabs (Laidre 2011). Shelters are beneficial not only as an efficient measure to reduce predation risk, but may have additional functions such as thermoregulation, which seems to be one reason why many cave-nesting birds also use nest boxes as roosting sites outside the breeding season (Mainwaring 2011). Similarly, small lemurs on Madagascar also make use of thermoregulatory benefits when choosing tree holes as sleeping sites (Schmid 1998; Dausmann et al. 2004; Lutermann et al. 2010). Regardless of which important functions burrows or shelters serve, competitors should be kept at bay (Takahashi et al. 2001; Smyers et al. 2002; Koga & Satoshi 2010; Morgan & Fine 2020).

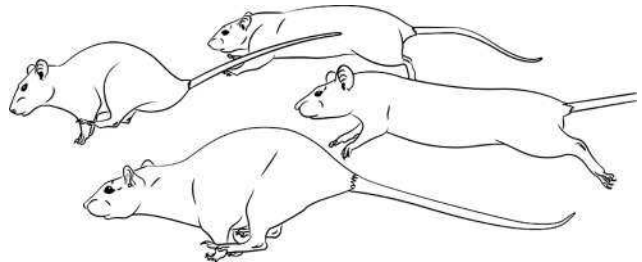


## (b) Share

Often, shelters may be sharable without noteworthy costs. If the benefits of sharing outweigh the costs, monopolizing shelters seems unprofitable, which may lead to joint use of roost sites, such as typically shown in bats (Kunz 1982; Kerth 2008), or of burrow systems, such as in fossorial rodents (Santos & Lacey 2011; Lacey et al. 2019). Thermoregulatory benefits may also select for grouping in shelters (Gilbert et al. 2010), as for instance in hibernating marmots (Arnold 1988, 1990b) and socially roosting birds (Paquet et al. 2016) and primates (Eppley et al. 2017; Campbell et al. 2018).

### 1.2.3 Competition for Mates and Social Partners

Individuals competing for sexual or social partners, e.g. mates or collaborators, should usually either *race* to outcompete others by being there first, or *fight* to get privileged access. Sharing of mates with a same-sex partner is usually costly, particularly for males, because males often compete in a zero-sum fashion for the same total amount of obtainable paternity. If fitness interests are correlated between competitors, however, sharing partners may be beneficial (Packer 1977; Packer & Pusey 1982; Cant & Reeve 2002; Krakauer & DuVal 2011).



## (a) Race

In the mating competition it can be uneconomic to monopolize reproduction with particular sexual partners, because due to the time involved (i.e. opportunity costs), this may prevent successful reproduction with alternative mates (Herberstein et al. 2017). This applies particularly when there is little investment involved in obtaining mates or fertilizations, such as with external fertilization observed in aquatic environments (e.g. in pelagic broadcast spawners: Shapiro et al. 1988; Levitan 1995; Domeier & Colin 1997; Crimaldi 2012), leading to promiscuous mating patterns. Here, it may pay to release gametes in large quantities at the right time, i.e. when the gametes of the other sex are available (Babcock et al. 1986, 1992; Levitan et al. 1991; Levitan 1995; Kaniewska et al. 2015). Turbulence and water flow processes greatly influence the outcome of the gametic race (Crimaldi & Zimmer 2014). This situation selects for high investment in gonads