REVIEW

Inbreeding and the evolution of sociality in arthropods

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Abstract Animals have evolved strategies to optimally balance costs and benefits of inbreeding. In social species, these adaptations can have a considerable impact on the structure, the organization, and the functioning of groups. Here, we consider how selection for inbreeding avoidance fashions the social behavior of arthropods, a phylum exhibiting an unparalleled richness of social lifestyles. We first examine life histories and parental investment patterns determining whether individuals should actively avoid or prefer inbreeding. Next, we illustrate the diversity of inbreeding avoidance mechanisms in arthropods, from the dispersal of individuals to the rejection of kin during mate choice and the production of unisexual broods by females. Then, we address the particular case of haplodiploid insects. Finally, we discuss how inbreeding may drive and shape the evolution of arthropods societies along two theoretical pathways.

Keywords Arthropods · Haplodiploidy · Inbreeding avoidance · Social evolution

Introduction

Inbreeding is a primary factor defining the genetic structure of animal groups and populations (Keller and Waller 2002). On the one hand, inbreeding incurs important fitness costs to the progeny. Inbred mating increases homozygosity in offspring and favors the expression of deleterious recessive alleles, often resulting in a decline of fitness traits known as inbreeding depression (Charlesworth and Willis 2009). Costs of inbreeding depression are further amplified at the population level as high homozygosity reduces the evolutionary potentials of the populations and thus increases their susceptibility to fast changing environments (Cheptou and Donohue 2011). Therefore, many animals have evolved strategies to prevent (or reduce) the incidence of mating with their kin (Pusey and Wolf 1996). Mating with too genetically distant individuals can also reduce the fitness of the progeny and lead to an outbreeding depression, for instance through the disruption of coadapted gene complexes or local adaptations (Charlesworth and Willis 2009). However, opportunities for extreme outbreeding are rare in nature and few animals may avoid mating with their non-kin (Bateson 1978, 1983).

On the other hand, inbreeding has substantial positive effects on the parent's inclusive fitness by increasing their representation of genes identical by descent in future generations (Parker 1979; Kokko and Ots 2006). For instance, a female mated with her brother has a 50 % chance to transmit not only one but two gene copies to the offspring. As the cost of inbreeding depression and the kin-selected benefit of inbreeding do not necessarily cancel out, their balance determines whether individuals should actively avoid or favor mating with their kin (Parker 1979, 2006; Lehmann and Perrin 2003; Kokko and Ots 2006; Puurtinen 2011).

Whether animals should prefer or avoid inbreeding is particularly important in social species where close relatives frequently interact as inbreeding tolerance at the individual level potentially affects the structure and functioning of groups. Most knowledge about how social animals strike an optimal balance between inbreeding and outbreeding has been deduced from studies on birds and mammals (Blouin and Blouin 1988; Thornhill 1993; Pusey and Wolf 1996).

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However, growing evidence on social insects (Gerloff et al. 2003), mites (Tien et al. 2011), and spiders (Bilde et al. 2005) reveal the profound impact of inbreeding on the fitness, the physiology, and the behavior of arthropods too. These recent observations thus shed new lights on the role of inbreeding in the regulation of social interactions in a phylum exhibiting an exceptionally rich spectrum of social forms, from temporary aggregations (Costa 2006) to colonies of thousands of individuals working together as a "superorganism" (Hölldobler and Wilson 2009).

The aim of our review is to discuss the role of inbreeding as a major evolutionary factor driving and shaping the social biology of arthropods. First, we examine evolutionary models of inbreeding tolerance theory. Second, we illustrate the diversity of inbreeding avoidance mechanisms across many arthropod taxa. Third, we address the particular case of inbreeding in haplodiploid insects. Finally, we discuss how a more comprehensive understanding of inbreeding regulation strategies in arthropods might help in clarifying the intimate relationship between inbreeding and the evolution of sociality along alternate pathways.

Balancing inbreeding and outbreeding

Arthropods show a high variability in their tolerance to inbreeding. In some species, individuals mate preferentially with their kin [e.g., flour beetles *Tribolium castaneum* (Nilsson *et al.* 2002)], whereas in others kin are rejected [e.g., German cockroach *Blattella germanica* (Lihoreau *et al.* 2008) and the primitively social bee *Lasioglossum zephyrum* (Greenberg 1979)]. Variation is also observed within species, for instance between individuals from laboratory and natural populations [paper wasp *Polistes dominulus* (Liebert et al. 2010)]. Interpreting these differences is often difficult, as the selection pressures on inbreeding tolerance are hardly measurable empirically. However, several evolutionary models have been proposed.

Theory suggests that individuals should either avoid or favor inbred matings in order to balance the cost of inbreeding depression and the kin-selected benefit of inbreeding (Parker 1979, 2006; Lehmann and Perrin 2003; Kokko and Ots 2006; Puurtinen 2011). Because individuals from different sexes, different populations, and different species face different ecological and social environments to which they have to adapt, this balance should be flexible.

Classical models predict that inbreeding tolerance should vary around a threshold value determined by the cost of inbreeding (Parker 1979, 2006). Below this threshold, individuals should actively favor inbreeding, even when this results in substantial reduction in offspring fitness. Above this threshold, however, individuals should avoid inbreeding. Because males and females often invest differently in reproduction (Trivers 1972; Thornhill and Alcock 1983), the models suggest that inbreeding tolerance should vary between sexes, thus generating conflicts zones in which males and females interests differ (Parker 1979, 2006). For instance, when mating does not affect future mating opportunities, males should prefer mating with their sisters if inbreeding depression is less than two thirds, while females should avoid mating with their brothers if inbreeding depression is greater than one third (Parker 1979, 2006; Lehmann and Perrin 2003; but see Kokko and Ots 2006; Puurtinen 2011 for different values).

Mating opportunities are also expected to influence inbreeding tolerance levels and generate differences between individuals of the same sex. As the parental investment increase, tolerance to inbreeding should decrease and become minimum when the opportunity of cost of mating is maximum, for instance if a male loses an outbred offspring for every offspring gained by its sister (Parker 1979, 2006). In a comprehensive examination of this opportunity cost, Kokko and Ots (2006) distinguished between simultaneous mate choice, where individuals can immediately choose between related and unrelated partners, and sequential choice, where partners are encountered once at a time. Their model suggests that sequential choice should often generate much higher inbreeding tolerance than simultaneous choice, thus raising the importance of the social environments (mate encounter rate), in addition to inbreeding depression strength and kin selected-benefits, in determining inbreeding tolerance by individuals.

Inbreeding avoidance mechanisms

In contrast to theoretical research, empirical literature in arthropods has almost exclusively focused on inbreeding avoidance strategies (but see Jennions et al. 2004; Bilde et al. 2005; Peer and Taborsky 2005; Edvardsson et al. 2008; De Luca and Cocroft 2008; Thurin and Aron 2009; Robinson et al. 2012). These include precopulatory mechanisms, by which individuals avoid mating with kin, and postcopulatory mechanisms, whereby individuals invest differentially in reproduction depending on their relatedness with mating partners.

Dispersal

Dispersal of males or females from their natal group is a widespread strategy reducing risks of inbreeding in arthropods, especially in eusocial Hymenoptera (ants, some bees, and wasps) where individuals of one or a few genetic lineages occupy a common nest and the probability of inbreeding is high (Table 1).

In ants, males (drones) and reproductive females (gynes) from several neighbor nests often emerge simultaneously

Table 1 Examples of inbreeding avoidance through dispersal in arthropods

Species	Order	Inbreeding avoidance mechanism(s)	Reference
Bombus californicus	Hymenoptera	Natal dispersal	Goulson (2010)
Bombus rufocinctus	Hymenoptera	Natal dispersal	Goulson (2010)
Bracon hebetor	Hymenoptera	Adult female dispersal	Ode et al. (1995)
Daphnia pulex	Cladocera	Natal dispersal	Winsor and Innes (2002)
Scaptotrigona postica	Hymenoptera	Adult male dispersal	Paxton (2000)
Ection burchellii	Hymenoptera	Natal dispersal	Jaffé et al. (2009)
Hyalophora cecropia	Lepidoptera	Adult male dispersal	Waldbauer and Sternburg (1979)
Ropalidia marginata	Hymenoptera	Adult male dispersal	Shilpa et al. (2010)
Trigona fuscobalteala	Hymenoptera	Adult male dispersal	Cameron et al. (2004)
Trigona sapiens	Hymenoptera	Adult male dispersal	Cameron et al. (2004)
Trigona collina	Hymenoptera	Adult male dispersal	Cameron et al. (2004)
Xylosandrus germanus	Coleoptera	Adult male dispersal	Peer and Taborsky (2004)

and undergo large nuptial flights, thus greatly decreasing the probability of mating between closely related nestmates (Keller and Passera 1993; Keller and Fournier 2002). After mating, dispersion of females (queens) is constrained by the colony foundation system and reaches longer distances when the colony is founded by a single winged queen than when the foundation is ensured by a queen along with a group of wingless workers. Dispersion of drones, however, is always independent of the colony foundation system and reaches much larger distances (Jaffé et al. 2009).

In the honeybee *Apis mellifera* (Koeniger and Koeniger 2000) and in many species of stingless bees (Paxton 2000; Cameron et al. 2004), virgin adults do not disperse randomly. Matings occur at drone congregations that form close to nest entrances where gynes are attracted. Drones rarely join congregations next to their natal colony but tend to disperse away, thus reducing the probability of mating with their sisters (Paxton 2000; Cameron et al. 2004). In some bumblebee species (Goulson 2010) and in the primitively eusocial wasp *Ropalidia marginata* (Shilpa et al. 2010), drones leave their maternal colony and patrol flowers to find females. Therefore, mating takes place in flower patches that are potentially exploited by females from multiple colonies (Shilpa et al. 2010).

In ambrosia beetles (Scolytinae), mating occurs in brood chambers excavated in freshly dead trees (Peer and Taborsky 2004). These chambers are occupied by full-siblings, and flightless males were initially assumed to mate with their sisters (Peer and Taborsky 2004). However, because beetles from multiple families build galleries close to each other in the same trees or in adjacent logs, males can disperse on the bark surface and visit other gallery entrances, thereby reducing risks of mating with their sisters. When the postdispersal mating opportunities of males are high, female beetles bias their offspring sex ratio toward males and thus increase their inclusive fitness (Peer and Taborsky 2004).

Social recognition

A second mechanism by which arthropods can reduce the incidence of inbred matings is to discriminate kin from other group members, either using familiar cues (nestmate recognition) or cues correlated with relatedness (kin recognition) (Table 2).

The best-documented example of social recognition is the nestmate recognition of eusocial Hymenoptera. In these insects, recognition of colony identity is mediated by the coating of cuticular lipids (hydrocarbons) protecting the cuticle against desiccation and attacks from microorganisms (Blomquist and Bagnères 2010). Additional cues such as hydrocarbons from the postpharyngeal glands in ants (Soroker et al. 1994), wax comb in bees (Breed 1998), or paper nest in wasps (Gamboa et al. 1986) can also be involved. These chemical compounds are exchanged and homogenized among colony members during food exchanges (trophallaxy) and/or physical contacts (allogrooming), generating a colony odor shared by all nestmates (van Zweden and d'Ettorre 2010). Individuals bearing identical or highly similar chemical signatures are recognized as nestmates, whereas individuals bearing different signatures are treated as non-nestmates. Nestmate recognition plays a fundamental role in the regulation of social interactions and the prevention of intrusions of strangers into the nest. Several evidences in bumblebees (*Bombus bifarius*, *Bombus frigidus*, and *Bombus terrestris*) indicate that nestmates recognition is also an efficient mechanism for inbreeding avoidance during mate choice (Foster 1992; Whitehorn et al. 2009).

Kin recognition is much less common in social arthropods (Fellowes 1998), presumably because the costs of nepotistic conflicts between non-sibling nestmates would

Table 2 Examples of inbreeding avoidance through social recognition in arthropods

Species	Order	Inbreeding avoidance mechanism(s)	Reference(s)
Argiope bruennichi	Araneae	Kin recognition	Welke and Schneider (2010)
Blattella germanica	Blattaria	Kin recognition	Lihoreau et al. (2007)
Bombus frigidus	Hymenoptera	Nestmate recognition	Foster (1992)
Bombus bifarius	Hymenoptera	Nestmate recognition	Foster (1992)
Bombus terrestris	Hymenoptera	Nestmate recognition	Whitehorn et al. (2009)
Bracon hebetor	Hymenoptera	Kin recognition	Ode et al. (1995)
Iridomyrmex humilis	Hymenoptera	Nestmate recognition	Keller and Passera (1993)
Lasioglossum zephyrum	Hymenoptera	Kin recognition	Smith and Ayasse (1987)
Lasioglossum malachurum	Hymenoptera	Kin recognition	Smith and Ayasse (1987)
Linepithema humile	Hymenoptera	Nestmate recognition	Keller and Fournier (2002)
Polistes dominulus	Hymenoptera	Nestmate recognition	Liebert et al. (2010)
Polistes fuscatus	Hymenoptera	Nestmate recognition	Gamboa et al. (1986)
Tetranychus urticae	Trombidiformes	Kin recognition	Tien et al. (2011)

impair colony efficiency in many eusocial species (Ratnieks et al. 2006). Nonetheless, kin recognition occurs in species exhibiting lower levels of social integration such as the gregarious cockroach *B. germanica* (Lihoreau et al. 2012). In this species, kin recognition is also mediated through the perception of cuticular hydrocarbons (Lihoreau and Rivault 2009). However, unlike eusocial Hymenoptera, cockroaches do not homogenize their chemical profiles. Rather, genetically determined variation of the relative abundance of the 25 hydrocarbons composing the cuticular profile of each individual allow cockroaches to discriminate their full-siblings in aggregates composed of familiar individuals from multiple genetic lineages (Lihoreau and Rivault 2009). Kin recognition allows *B. germanica* males and females to avoid inbred mating based on a mutual mate choice (Lihoreau et al. 2007; Lihoreau et al. 2008; Lihoreau and Rivault 2010). A similar kin recognition system has been described in the primitively eusocial bees *L. zephyrum* (Greenberg 1979) and *Lasioglossum malachurum* (Smith and Ayasse 1987). Although the precise nature of the recognition cues has not been identified in these species, kin recognition is mediated through chemical cues. Males habituate to the odor of females and avoid mating with those carrying familiar scents (Smith and Ayasse 1987).

In some other species, kin recognition allows individuals to adjust their mating investment in relation to their relatedness with partners. For instance, males of the Indian meal moth *Plodia interpunctella* can mate up to eight times during their short lifetime and provide fewer sperm to their sisters than to less closely related partners (Lewis and Wedell 2009). Similar cryptic mate choice by males occurs in the orb-web spider *Argiope bruennichi* where males shorten the duration of copulation when mating with a sibling female (Welke and Schneider 2010). This strategy may enable spider males to escape sexual cannibalism and increase their chances of remating with a less-related female (Welke and Schneider 2010).

Polyandry

If females cannot avoid copulating with their kin, multiple mating increases the probability of producing some outbred progenies under random copulation and thus enhances their fitness (Stockley et al. 1993; Cornell and Tregenza 2007). Accumulating evidence shows that relatedness is also an important factor determining if a given sperm will fertilize an egg through active discrimination or cryptic postmating mechanisms (Table 3). For instance, in the field cricket *Gryllus bimaculatus*, females avoid inbreeding by preferentially fertilizing their eggs with sperm from unrelated males (Tregenza and Wedell 2002; Bretman et al. 2004). Whether females impose their choice by accepting less sperm from closely related males or by reducing the fertilization success of sperm from related males remains unknown (Tregenza and Wedell 2002). Sperm count in the spermathecae of female crickets mated both with a sibling male and a non-sibling male shows that the sperm of the non-sibling is preferentially stored and that the relative amount of sperm in storage reflects future paternity (Bretman et al. 2009). In *Teleogryllus oceanicus* (Simmons et al. 2006) and *Teleogryllus commodus* (Bussière et al. 2006), females actively discriminate unattractive males by removing their spermatophores before insemination can be completed.

A particular effect of polyandry on the reproductive success of individuals has been reported in the migratory locust *Locusta migratoria* (Teng and Kang 2007). In this species, the eggs of females mated with one sibling male only have lower hatching success than the eggs of females mated with both a sibling male and a non-sibling male. There is no evidence that females bias paternity toward

Table 3 Examples of inbreeding avoidance through polyandry in arthropods

Species	Order	Inbreeding avoidance mechanism(s)	Precopulation mechanism	Postcopulation mechanism	Reference(s)
Apis mellifera	Hymenoptera	Polyandry	+	−	Page (1980)
Drosophila melanogaster	Diptera	Sperm selection	−	+	Mack et al. (2002)
Ection burchellii	Hymenoptera	Polyandry	+	−	Jaffé et al. (2009)
Ephestia kuehniella	Lepidoptera	Polyandry	+	−	Xu and Wang (2009)
Gryllodes sigillatus	Orthoptera	Polyandry	+	−	Xu and Wang (2009)
Gryllus bimaculatus	Orthoptera	Sperm selection	−	+	Tregenza and Wedell (2002)
Locusta migratoria	Orthoptera	Maternal effects	+	+	Teng and Kang (2007)
Oedothorax apicatus	Araneae	Polyandry	+	−	Bilde et al. (2005)
Plodia interpunctella	Lepidoptera	Differential sperm investment	−	+	Lewis and Wedell (2009)

non-sibling males. Rather, male locusts transfer nutritional compounds (proteins) to the eggs through their ejaculates and variations in the composition of these proteins among males may simply enhance the hatchability of eggs fertilized by sibling males by providing them with a richer composition of nutrients (Teng and Kang 2007). A similar pattern of sperm investment has been found in the fruit fly *Drosophila melanogaster* where sperm competitive ability is negatively correlated with relatedness. However, the role of cryptic female choice in this species cannot be disregarded (Mack *et al.* 2002). In the Mediterranean flour moth *Ephestia kuehniella* (Xu and Wang 2009) and in the cricket *Gryllodes sigillatus* (Ivy et al. 2005), females avoid inbreeding by discriminating the males they previously mated with and selecting new mates for subsequent copulations.

Monogeny

Monogeny is an unusual sex determination system in several species of gall midges, sciarid flies, coccids, isopoda, and cynipid wasps (Werren et al. 2002), where all offspring of a female are either exclusively males or females. Despite having received little attention in the context of inbreeding avoidance, monogeny is potentially an important mechanism preventing inbred matings in arthropods (Tabadkani et al. 2012a, b). The unique sex determination system in monogenous arthropods is either genetically based (Stuart and Hatchett 1991) or a result from the action of symbiotic microorganisms (Abe and Miura 2002). In gall midges, for instance, a single maternal-effect autosomal gene called chromosome maintenance (*Cm*) prevents the elimination of the X chromosome during embryogenesis. *Cm*-bearing females obtain a female-determining karyotype and produce only female offspring, while *Cm*-lacking females obtain a male-determining karyotype and produce only male offspring (Stuart and Hatchett 1991).

In monogenous midges, all offspring of a female are exclusively unisexual and live in galls or patches of their prey. Thus, offspring of each female inevitably mate with those of other females that are non-siblings or in the worst case half-siblings (common father and two different mothers). A recent study suggests that monogeny can lead to decreased inbreeding frequency and increased individual fitness (Tabadkani et al. 2011). Simulation models of inbreeding coefficients in monogenous and non-monogenous populations (for gall midges in which males mate multiply times but females are monandrous) predict that average inbreeding coefficients per individual should not differ between populations over generations. However, the maximum inbreeding coefficient should be lower in monogenous populations. By avoiding mating with full-siblings, monogenous gall midges postpone the effects of inbreeding depression. This delay is expected to be especially important in species with few annual generations as individuals of the last generation have higher fitness and less mortality rate associated with inbreeding depression during the overwintering period (Tabadkani et al. 2011).

Inbreeding avoidance in haplodiploid insects

Particular to the study of inbreeding avoidance in arthropods is the case of haplodiploid species. In most haplodiploid hymenopterans (ants, bees, sawflies, and wasps), a single-locus complementary sex-determination system (sl-CSD) controls the production of males and females (Whiting 1943). Heterozygotes for this locus become females, while hemi- and homozygotes become haploid and diploid males, respectively (Elias et al. 2009).

In principle, haplodiploid species should suffer less from inbreeding than diploid species due to purging of deleterious recessive alleles in haploid males (Henter 2003). However, a

body of evidence indicates that the overall cost of inbreeding is in fact higher in haplodiploid species (Zayed and Packer 2005). First, purging of deleterious alleles may not be effective against female sex-limited traits, such as hibernation survival, colony foundation success, and fecundity (Gerloff and Schmid-Hempel 2005; Schrempf et al. 2006), as suggested for example by low fecundity, overwintering survival, and colony size in inbred lineages of the bumblebee *B. terrestris* (Beekman *et al.* 1999; Gerloff and Schmid-Hempel 2005). Second, and perhaps more importantly, the sl-CSD system generates an unusual source of genetic load through the production of unviable or sterile diploid males issued from fertilized eggs homozygous at the sex-determining locus (Zayed and Packer 2005; Goulson 2010). Large haplodiploid populations can maintain many alleles in their sex-determination locus and thus have low levels of diploid male production. However, in small populations, high inbreeding rates reduce sex locus allelic diversity and increase the production of diploid males (Zayed and Packer 2005). For example, a female mating with a male who shares one of her sex-determining alleles will produce a colony in which 50 % of the members are diploid males (Bourdais and Hance 2009). In some eusocial Hymenoptera, such as honeybees and ants, diploid male larvae are killed by workers. In others however, such as bumblebees and paper wasps, diploid males are reared to adulthood (Gerloff et al. 2003). In these species, the mating between diploid males and diploid females results in the production of sterile triploid progenies. These sterile individuals constitute a genetic load and their accumulation in the population is therefore a potential trigger of a rapid extinction vortex (Zayed and Packer 2005).

Given the elevated costs of inbreeding associated with this genetic load, selection for mechanisms limiting the incidence of inbred mating should be stronger in haplodiploid species that reproduce by sl-CSD than in species with multilocus complementary sex determination in which the production of diploid males is much lower (Bourdais and Hance 2009). This argument is supported by the large diversity of inbreeding avoidance mechanisms encountered in haplodiploid hymenopterans (see examples in Tables 1, 2, and 3). In some species, such as the wasps *Trichogramma kaykai* (Stouthamer *et al.* 2001) and *Nasonia vitripennis* (Nur et al. 1988), a modification of paternal chromosomes enables diploid males to produce fertile progeny, minimizing the costs associated with production of diploid males. In these species, the elimination of one set of paternal chromosomes during mitosis of the triploid zygote results in a normal diploid zygote that eventually develop into a diploid daughter (Elias et al. 2009). Because inbreeding has potentially fewer adverse effects under non-complementary sex determination systems rather than sl-CSD, it is also not surprising to observe evolutionary transitions from sl-CSD to non-complementary sex determination in many hymenopteran species as for instance in the chalcidoid and braconid wasps (Beukeboom et al. 2000).

Inbreeding and the evolution of sociality

Above we have presented some of the evidence illustrating how selection for inbreeding avoidance impacts the fitness, the physiology, and the behavior of arthropods. We now discuss how a more comprehensive understanding of the strategies used by arthropods to optimally balance inbreeding and outbreeding might help in clarifying the role of inbreeding in social evolution in this phylum.

Since Hamilton's formalization of inclusive fitness theory (Hamilton 1964), inbreeding has been recognized as a principal factor of social evolution (Bourke 2011). Inbreeding (even mild) increases within-group relatedness and therefore favors the evolution of cooperation and advanced forms of sociality by means of kin selection (Abbot et al. 2011; Strassman et al. 2011; Fig. 1). Over the past decades, empirical validations of this prediction have gone hand-in-hand with the study of the social arthropods and it is now well accepted that independent evolutions of eusociality in ants, bees, and wasps have always been preceded (or coincided) with high relatedness (Hughes et al. 2008). In these lineages, lifetime monogamy has set the stage for the evolution of a complex suite of social traits, often leading to a "point of no return" in highly integrated societies where individuals from different castes have distinct anatomies and cannot develop outside a social context (Wilson and Hölldobler 2005).

However, social life itself inevitably amplifies the probability of inbred matings, thus selecting for incest avoidance strategies in species where the costs of inbreeding depression exceed the benefits of kin selection (Parker 1979, 2006; Lehmann and Perrin 2003; Kokko and Ots 2006; Puurtinen 2011). Therefore, inbreeding constitutes both a cause and a consequence of social evolution. As illustrated throughout this review, social arthropods have evolved a range of inbreeding avoidance mechanisms that have profound impacts on the structure, the organization, and the functioning of groups by acting upon the physiology and behavior of individuals (Fig. 1). For instance, sex-biased dispersal and monogeny define the composition of groups. These adaptations to inbreeding bias the proportion of males and females that are sexually available (the operational sex ratio) and thus potentially favor the evolution of mating systems with highly asymmetric sex roles and dominance hierarchies. Nestmate and kin recognition, by which individuals can actively avoid to mate with their kin, favor natal phylopatry and might facilitate the establishment of large permanent colonies composed of individuals from multiple genetic
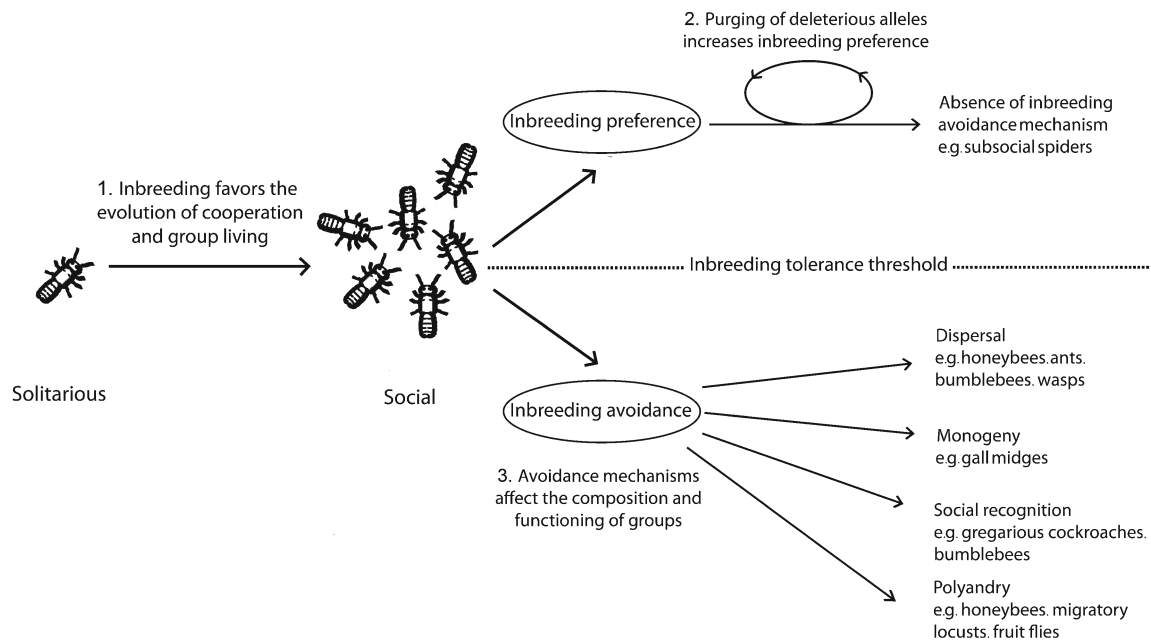
Fig. 1 Theoretical diagram illustrating how inbreeding could affect the evolution of social behaviors. *1* In the early stages of socialization, inbreeding drives the evolution of cooperation and group-living via the action of kin selection. However, as animals go from solitarious to social, their risks of incurring high costs of inbreeding depression increase as closely related individuals are more likely to encounter and mate. We suggest that inbreeding tolerance by individuals, as defined by the balance between the kin-selected benefits of inbreeding and the costs of inbreeding depression, determines two pathways for sociality. *2* If the costs of inbreeding depression are lower than the benefits of kin selection, a long history of inbreeding and the purging of deleterious alleles should further promote the evolution of sociality by kin selection. This scenario has been proposed to explain the transition from subsociality to sociality in spiders. *3* Alternately, if the costs of inbreeding depression are higher than the benefits of kin selection, individuals should evolve mechanisms to avoid (or reduce) inbreeding as observed in various arthropods (Tables 1–3). These mechanisms have a profound impact on the composition and the functioning of social groups and reduce the evolutionary potential of sociality via kin selection, thus shaping the social biology of species. In arthropods, inbreeding avoidance mechanisms include dispersal, kin recognition, polyandry, and monogeny

lineages. Polyandry increases the genetic diversity among group members and enhances group level fitness traits necessary to succeed in unstable ecological conditions as suggested in honey bees where genotypically diverse colonies had greater resistance to disease (Seeley and Tarpy 2007), more stable nest thermoregulation (Jones et al. 2004), and higher productivity (Mattila and Seeley 2007) than genotypically similar colonies.

Interestingly, however, if a population has already undergone a long history of inbreeding, purging of deleterious recessive alleles should reduce the magnitude of inbreeding depression and thus increase tolerance to inbreeding (Glémin 2003). This self-reinforcing process, well known in plant literature (Lehtonen and Kokko 2012), has been recently described in various arthropods (Swindell and Bouzat 2006; Facon et al. 2011) and should in principle further promote the evolution of sociality by kin selection (Fig. 1). This hypothesis has been proposed to explain the evolution of sociality in spiders (Bilde et al. 2005). A long inbreeding history due to the lack of inbreeding avoidance in subsocial spiders may have facilitated the evolution of inbreeding tolerance and driven the transition to regular inbreeding observed in social species, where individuals

form stable and highly inbred colonies with overlapping generations (Bilde et al. 2005). This argument is not specific to spiders but could also explain the evolution of sociality in several other taxa in which inbreeding is the rule rather than the exception, such as bark beetles (Keller et al. 2011) and termites (Goodisman and Crozier 2002).

Examining these two potential evolutionary pathways for sociality constitutes an exciting challenge for future studies on inbreeding in arthropods. Work in this direction should focus on testing the predictions of evolutionary models of inbreeding tolerance (Parker 1979; Kokko and Ots 2006) based on empirical measures of inbreeding depression and life history traits (such as parental investment, mating opportunities, and inbreeding history) to determine how ecological conditions, social environments, and population dynamics define levels of inbreeding tolerance by individuals, sexes, population, and species. Arthropods hold considerable promises to conduct this comparative research because they exhibit a rich diversity of social forms that are relatively easy to manipulate and to rear in laboratory conditions. Recent advances in molecular biology now also provide tools to assess the genetic structure of populations

and explore these questions in the wild (Allendorf et al. 2010; Kristensen et al. 2010). Ultimately, we hope that a better recognition of inbreeding as a major factor driving and shaping social evolution will help clarify the evolutionary pathways that have led to the diversity of social lifestyles observed in arthropods and in other animals.

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