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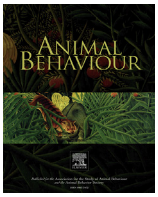

Review

The keystone individual concept: an ecological and evolutionary overview

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The concept of keystone individuals offers a unifying framework to study the evolution and persistence of individuals that have a disproportionately large, irreplaceable effect on group dynamics. Although the literature is teeming with examples of these individuals, disparate terminologies have impeded a major synthesis of this topic across fields. To allow a strict classification of potential keystone individuals, we offer herein some general terminology, outline practical methodological approaches to distinguish between keystone individuals and generic individuals that only occupy a keystone role, and propose ways to measure the effect of keystones on group dynamics. In particular, we suggest that keystone individuals should be classified as 'fixed' or 'episodic' according to the duration of time over which they impact their group. We then venture into the existing literature to identify distinctive keystone roles that generic and/or keystone individuals can occupy in a group (e.g. dominant individual, leader or superspreader), and describe traits that can give rise to keystone individuals. To highlight the ecological implications, we briefly review some of the effects that keystone individuals can have on their group and how this could affect other levels of organization such as populations and communities. In looking at their diverse evolutionary origins, we discuss key mechanisms that could explain the presence of keystone individuals. These mechanisms include traditional Darwinian selection on keystone-conferring genotypes, experience and state- or context-dependent effects. We close our review by discussing various opportunities for empirical and theoretical advancement and outline concepts that will aid future studies on keystone individuals.

A well-established tenet in community ecology is that disproportionalities exist in the strength with which species impact their environment. In some cases, one species can singly play such a fundamental functional role that its presence/absence effectively changes the way whole communities or ecosystems appear and operate. The concept of these 'keystone species', which are defined as having a disproportionately large effect on community dynamics relative to their abundance, has been widely reinforced, although often criticized, since its conception by Robert Paine (Mills, Soule, & Doak, 1993; Paine, 1969, 1995; Power et al., 1996). Like interspecific variation, trait variation occurring at the level of the individual can have subtle but equally profound ecological consequences. For instance, intraspecific differences can impact individuals' fitness, drive population vital rates, shape biological communities, or alter the dynamics of entire ecosystems (Bolnick et al., 2003, 2011). Until recently, however, such variation has been largely ignored by ecologists or treated as mere statistical noise. In contrast, the last decade has seen a surge in the number of papers devoted to ecological effects of individual variation (Dall, Bell, Bolnick, & Ratnieks, 2012; Dall, Houston, & McNamara, 2004; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Violle et al., 2012; Wolf & Weissing, 2012). Impressively, in many test systems, the effect sizes of individual variation can resemble or even exceed those ascribed to interspecific differences. It follows that, if (like species) individuals vary in their ecological impact, the keystone species concept could be applied to individuals, where a subset of individuals have a disproportionately large effect on local group dynamics.

Several subfields of behavioural ecology and population biology alike have seemingly independently developed terms to describe highly influential individuals. Yet, an overarching framework for their study has never been rigorously applied. One reason for the lack of conceptual development is that the phenomenon has often been treated as an idiosyncratic storytelling or a sort of semi-scientific anecdote, rather than as a reasonably common

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phenomenon with important ecological and evolutionary implications. Instead, divergent terminologies and a lack of a uniting framework have prohibited major synthesis of this concept across fields. For instance, Robson and Traniello (1999) recognized the importance of 'key individuals' for social insect colonies and classified several types according to their specific function within the group. These authors further emphasized the need to study behaviour at the individual level in order to understand the organization of group behaviour, because cooperative behaviours might be differentially performed by a narrow subset of specialized or 'elite' individuals. Various terms have been used to describe particularly influential individuals in different systems and circumstances ('elites': Pinter-Wollman, Hubler, Holley, Franks, & Dornhaus, 2012; 'superspreaders': Meyers, Pourbohloul, Newman, Skowronski, & Brunham, 2005; Paull et al., 2011; 'leaders': McComb et al., 2011; Reebs, 2000; 'dominants': Ballard & Robel, 1974; Clarke & Faulkes, 1997; 'alphas': Bernstein, 1969; 'tutors': Knörnschild, Nagy, Metz, Mayer, & von Helversen, 2010; no specific term: Alberts, Sapolsky, & Altmann, 1992). Although these words have subtly different definitions or connotations, the feature that they share in common is that they all describe individuals with an inordinately large influence on surrounding conspecifics (Table 1). Here we argue that this feature unites these individuals in an important way, and that questions pertaining to how such individuals evolve and how they impact their groups/populations could profitably be viewed in a shared organizational framework. Here, we largely focus on how keystone individuals influence group dynamics, because this is the scale at which we presently have the most data and the deepest understanding.

The term 'keystone individuals' was first drawn by Sih and Watters (2005) to explain the inordinate effect that some individuals exert on group dynamics and performance. After Sih and Watters (2005), we will herein refer to such highly influential individuals as 'keystone individuals' because (1) the term bears thematic resemblance to the keystone species concept, (2) the term is agnostic to the kind of influence these individuals have on groups and (3) it has intuitive appeal.

KEYSTONE INDIVIDUALS DEFINED

The keystone individual concept resembles the keystone species concept (sensu Power et al., 1996) in its basic properties: both entities have a large effect on their living environment relative to their abundance. Following the description of Sih and Watters (2005, pp.

Table 1
Empirical examples of keystone roles for various taxa at the group level and the population level

Taxon	Keystone role	Description	Reference
Group level			
Eusocial insects			
Temnothorax albipennis	Performer	Performers are more essential in small colonies	Dornhaus et al. (2008)
T. albipennis, *T. rugatulus*	Elite	Elites perform all or many tasks efficiently	Pinter-Wollman et al. (2012)
T. albipennis	Leader	Knowledgeable individuals lead collective decision making	Stroeymeyt et al. (2011)
Apis mellifera	Catalyst	Removal of catalysts led to elongated dispersal latency and/or aborted liftoff attempts	Donahoe et al. (2003)
Formica schaufussi	Organizer	Scouts organize prey retrieval, and \removal of organizer halts collective behaviour	Robson and Traniello (2002)
Noneusocial insects			
Water strider, *Aquarius remigis*	Hyperaggressive male	Hyperaggressive individuals strongly depress overall group dynamics	Chang and Sih (2013); Sih and Watters (2005)
Fish			
Mosquitofish, *Gambusia affinis*	Disperser	The boldest individuals dispersed the furthest; new population is contingent on disperser behaviour	Cote et al. (2010)
Zebrafish, *Danio rerio*	Performer	Removal of key fish reduces performance in a group-foraging learning task	Vital and Martins (2011)
Birds			
Greater prairie chicken, *Tympanuchus cupido*	Dominant male	Removal of dominant males led to immense decrease of group reproductive success	Ballard and Robel (1974)
Mammals			
Sac-winged bat, *Saccopteryx bilineata*	Tutor	Male tutors 'teach' complex vocalizations to the pups in their harem via vocal imitation	Knörnschild et al. (2010)
African elephant, *Loxodonta africana*	Key individual	The presence of a knowledgeable matriarch increases group knowledge via discrimination	McComb et al. (2001)
Naked mole-rat, *Heterocephalus glaber*	Queen	The queen suppresses reproduction of other females, and her removal leads to social instability	Clarke and Faulkes (1997)
Bottlenose dolphin, *Tursiops truncatus*	Broker	Key individuals are crucial for the cohesion of the community	Lusseau and Newman (2004)
Pigtailed macaque, *Macaca nemestrina*	Conflict manager, policer	Maintain social order	Flack et al. (2005); Flack et al. (2006)
Yellow baboon, *Papio cynocephalus*	Hyperaggressive male	Immigration of one hyperaggressive male had strong negative effects on the group	Alberts et al. (1992)
Capuchin monkey, *Cebus albifrons*	Controller	Controller defends group from disturbance and terminates most intragroup conflict	Bernstein (1966)
Population level			
Human, *Homo sapiens*	Superspreader	Superspreaders have inordinately high disease transmission and rapid outbreak patterns	Meyers et al. (2005); Paull et al. (2011)
Oleander aphid, *Aphis nerii*	Superclone	A single genotype dominates habitats across long distances (3700 km) and across years	Harrison and Mondor (2011)

See Supplementary material (Table S1) for an expanded version of this table.

1427–1428), we define a keystone individual as an ‘individual that has a disproportionally large, irreplaceable effect on other group members and/or the overall group dynamics relative to its abundance’.

We differentiate keystone individuals from mere generic individuals that occupy a ‘keystone role’ via their irreplaceability. A keystone role is defined herein as a role or function of high importance that an individual or small set of individuals occupies. These individuals could be keystone individuals, generic individuals or a mixture of both. Differentiating a keystone individual from a generic individual currently occupying a keystone role requires a simple removal experiment (Sih, Hanser, & McHugh, 2009). While the removal of a keystone individual would have profound and lasting consequences for group dynamics, the removal of a generic individual in a keystone role would only have intermittent performance consequences that would only last for as long as it takes for another generic individual to take that role. The reason for this would be that a keystone individual has a more pervasive, individually unique influence that cannot be replaced by a mere generic individual. In both cases, the removal of the putative keystone must be compared against control removals of another generic group member.

We further clarify keystone individuals in terms of the consistency with which they influence their groups. Depending on the constancy of their role in the group, keystone individuals can be defined as either ‘fixed’ or ‘episodic’. Fixed keystone individuals consistently inhabit a highly influential role in the group for long periods (e.g. alpha males in pigtailed macaques, *Macaca nemestrina*; Bernstein, 1969). In contrast, episodic keystone individuals influence groups only for restricted periods (e.g. due to experiential factors; Stroeymeyt, Franks, & Giurfa, 2011) or during an intermittent physiological state (Krause, 1993). For example, a single scout in *Formica schaufussi* ants can become an episodic keystone individual during a foraging event if it encounters a prey item that is too large to retrieve individually and hence organizes a retrieval group (Robson & Traniello, 2002). However, the scout’s influence expires after its knowledge has been exploited by other group members. Robson and Traniello (2002) further noted that if the keystone scout was removed during the retrieval event, the group lost its cohesion and the recruited workers (other scouts) abandoned the prey, thus terminating the cooperative behaviour. Hence, although an episodic keystone’s effect directly occurs over a short period, its impact could be long-term and critical. Notably, the terms ‘fixed’ and ‘episodic’ refer to extremes along a continuous spectrum, and thus, in many systems keystone individuals may lie intermediately along this continuum.

METHODS FOR TESTING THE PRESENCE OF KEYSTONE INDIVIDUALS

Basic Observation

The first step to identifying and measuring the effect of keystone individuals is detailed observation. Descriptions of individual behavioural patterns and the effects that they seem to have on group dynamics are often our first clues to which (if any) individuals have a large effect on group dynamics. Once equipped with these clues, investigators can then compare the performance of groups containing versus lacking putative keystones to further explore their effects on group dynamics. Ideally, such removals would be experimental in nature, but even when they are not, serendipitous observational data can provide powerful inferences. For example, a study on olive baboon, *Papio anubis*, troops showed that the death of the more aggressive males (due to tuberculosis infection) resulted in a shift in group temperament to a more pacific culture that persisted for more than a decade (Sapolsky & Share, 2004). While this constitutes an excellent example of how the removal of keystone individuals can impact within-group interactions, it also demonstrates some of the drawbacks of observational studies. First, depending on the species, observations must often be carried out over extended periods, and are therefore highly laborious. Second, observational studies will not necessarily expose keystone individuals, particularly if identification requires the removal or death of the individual. For instance, without the fortuitous death of the aggressive males, Sapolsky and Share (2004) may not have been able to observe changes in the group culture. Many observers will not be so lucky. Third, even in their fortuitous study, Sapolsky and Share’s conclusions are confounded between two or more variables: loss of keystone individuals and a change in group size.

The latter problem can be avoided by using intergroup comparisons. For example, Chang and Sih (2013) compared 64 experimentally constructed groups of water striders, *Aquarius remigis*, and found that the prevalence of hyperaggressive males (the keystone individuals) had major impacts on mating dynamics in the overall group. Beyond identifying keystone individuals per se, if they are common and easy to identify, one can compare the traits of individuals occupying keystone roles in multiple groups. This is intriguing, because the success of the group and many of the social dynamics therein might be associated with the traits of the keystone individuals (e.g. McComb et al., 2011). However, if the focal trait is the behavioural type of the keystone individual, intergroup comparisons may not reveal whether groups members adjust their behaviour according to the behavioural type of their keystone individual or vice versa. Thus, although observational data can provide clues to the mechanisms governing group dynamics, only controlled manipulations of group composition can illuminate the cause/effect relationship.

Controlled Manipulation

In contrast to keystone species, keystone individuals are far easier to remove, return or replace in manipulation experiments. Once a potential keystone individual is identified, a comparison of group tasks/performance between (1) a group where a potential keystone is removed versus (2) a control group where a random individual is removed can reveal whether an individual is a true keystone or whether it is merely the current occupant of a keystone role (Fig. 1). For example, removal experiments have revealed that during nest relocation, highly active ‘elite’ workers in *Temnothorax* ants are quickly replaced by other generic workers that were previously less active (Pinter-Wollman et al., 2012). Consequently, an ‘elite’ worker would be a description for a keystone role that could be taken by other generic individuals and not for a true keystone individual. Notably, in the case of an episodic keystone individual, the removal is time-sensitive (i.e. the individual has to be removed during its time of influence, such as during organization of a prey retrieval group; Robson & Traniello, 2002). If a keystone role is associated with a specific behavioural type, like in hyperaggressive water striders (Sih & Watters, 2005), experimentally varying group compositions with different proportions of the focal behavioural type could be compared to examine both the individual and group consequences to estimate interaction strengths (Chang & Sih, 2013). Alternatively, keystone individuals with differing behavioural types could be switched among groups (e.g. aggressive leaders could be replaced with docile leaders). Thereby, one could analyse whether the focal behavioural types of the keystone individuals are associated with group dynamics and whether groups take on the behavioural traits of their new keystone individual or vice versa. This latter approach would be the natural, experimental

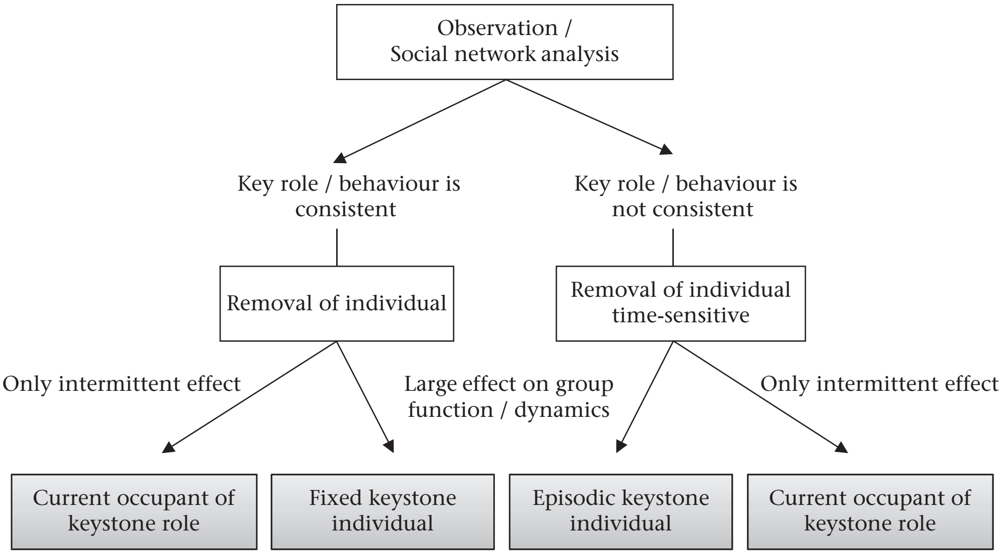

Figure 1. Path diagram illustrating removal experiments to distinguish keystone individuals from generic individuals that only occupy a keystone role. In the case of putative episodic keystone individuals, removal experiments are time-sensitive (i.e. they must be performed while the individual is influencing the group).

complement to the intergroup comparison methodology described previously. To avoid modifying group structure, one could also manipulate the behaviour of putative keystone individuals chemically (i.e. using hormones or drugs).

Social Network Theory

Social network theory provides another set of tools to identify and analyse keystone individuals and their impacts on group dynamics (Sih et al., 2009; Wey, Blumstein, Shen, & Jordan, 2008). Measures like ‘degree’, the number of individuals with which an animal interacts, and ‘centrality’ give us estimates of how well connected individuals are with other group members and can be used to identify individuals that represent ‘keystone nodes’, such as highly connected individuals in zebrafish, *Danio rerio* (Vital & Martins, 2011), brokers in bottlenose dolphins, *Tursiops truncatus*, that connect subpopulations (Lusseau & Newman, 2004) or conflict mediators in pigtailed macaques (Flack, Girvan, de Waal, & Krakauer, 2006; Flack, Krakauer, & de Waal, 2005). Furthermore, social network metrics can be used to choose appropriate controls for keystone removal experiments (low-centrality individuals as a control for keystone node removal) as has been done in zebrafish (Vital & Martins, 2011). If direct manipulations are not possible, social network models might still be used to simulate keystone node removal. For instance, simulations could be used for wildlife management efforts involving social species like killer whales, *Orcinus orca* (Williams & Lusseau, 2006) or public health measures to counter disease outbreaks like SARS (Meyers et al., 2005).

EXAMPLES OF KEYSTONE INDIVIDUALS IN THE LITERATURE

Here, we describe some of the most captivating or thoroughly characterized examples, with the ultimate goal of conveying the diversity of test systems, circumstances and outcomes that can be shaped by the behaviour of one or a few keystone individuals. Note that for many examples, it has not yet been demonstrated whether these keystone roles are inhabited by true keystone or mere generic individuals. Only controlled removal experiments with extended observations of long-term effects would make it possible to determine whether the removal has intermittent or long-lasting effects on group dynamics.

Dominant or Alpha Individuals

The position of a dominant or an alpha individual may be among the most prominent examples for keystone roles in animal groups. Dominant individuals can emerge from one of several social processes. First, dominant individuals may emerge as a consequence of numerous, persistent agonistic interactions between group members (reviewed in Drews, 1993). These interactions serve to organize and reinforce a social hierarchy. Second, dominant individuals may emerge as a consequence of a small number of interactions that effectively shape how the dominant individual is perceived by fellow group members. Or, third, dominants may exert their influence via indirect routes, where their behaviour influences the behaviour of one group member (e.g. a member of its coalition or family), which in turn, causes a downstream change in the behaviour of other group members.

Dominant individuals often acquire a disproportionately large number of mating opportunities and resources, and their actions can have enormous impacts on the behaviour and physiology of other group members (Clarke & Faulkes, 1997). For example, in primates, alpha individuals help maintain social stability and defend the group against predators/intruders (Bernstein, 1969). Interestingly, such group-stabilizing individuals can also be present in societies lacking pronounced dominance hierarchies. In these cases, the individuals have been referred to as ‘control animals’ (Bernstein, 1966). Studies on pigtailed macaques have shown that the removal of control animals increases levels of aggression and decreases sociopositive interactions, like grooming and play (Flack et al., 2005). Similar dynamics have been observed in taxonomically divergent systems. For instance, in greater prairie chickens, *Tympanuchus cupido*, removal of dominant males from booming grounds (display areas) results in destabilized social organization: aggressive encounters increase and males are unable to maintain distinct territories, decreasing group mating success from 92% to only 13% (Ballard & Robel, 1974). Thus, the collective mating performance of entire groups may be dictated by the presence and behaviour of singular, influential group members. It is worth noting, however, that dominance is usually defined in terms of winning contests and is not a reliable indicator of an individual’s impact on its group, stressing the importance of experimental removals for determining dominants’ influence.

Keystone Nodes

Keystone nodes occur in two forms: (1) individuals that are highly connected and (2) individuals that do not necessarily have lots of connections, but play a key role in bridging two or more groups that are otherwise isolated. Due to high contact rates with other group members, highly connected individuals can increase the flow of information and/or resources among individuals, but may also pose a serious risk for their group, community or population if they contract an infectious disease (Naug, 2008). In the fields of disease ecology and epidemiology, these individuals have been termed 'superspreaders' (Meyers et al., 2005; Paull et al., 2011). Despite this obvious risk, groups and communities can also receive benefits from harbouring individuals with a high connectivity. For instance, Lusseau and Newman (2004) showed that populations of bottlenose dolphins contain 'brokers' that connect different subpopulations and thereby increase social cohesion of the whole population. Likewise, cohesion in killer whale social networks appears to rely on a limited number of female juveniles that hold central positions (Williams & Lusseau, 2006). Similar patterns have also been observed in more experimentally tractable systems. For instance, individuals occupying central roles in zebrafish networks have a larger influence on group movement, which enables them to use acquired personal information to increase their group's predator avoidance (Vital & Martins, 2013). In addition, a group's ability to learn tasks may rely on centrally located individuals: manipulation experiments in zebrafish revealed that only groups that retain their keystone individuals are able to associate a red card with food during staged-learning foraging challenges (Vital & Martins, 2011). Whether centrally located individuals could also impose costs to their groups (e.g. via the acquisition of incorrect or imperfect information) has not been as thoroughly examined.

Collective Decision Making

Although group decisions can have profound consequences for survival and fitness for each group member, group decisions are commonly made by only one or a few individuals, sometimes referred to as 'leaders' (e.g. foraging movement in golden shiner, *Notemigonus crysoleucas*, fish shoals: Reebs, 2000; nest relocation in honeybee, *Apis mellifera*, swarms: Seeley, Morse, & Visscher, 1979). Even in behaviours that seem completely collective and decentralized (e.g. nest choice in ants) a few leaders can effectively make the decision for the entire colony (Stroeymeyt et al., 2011). Whether or not the group benefits from these decisions depends on the leader's abilities. Many social societies (including humans) profit from the preservation of older individuals that act as information repositories. For example, elephant groups with older matriarch leaders possess not only a higher social discriminatory ability, but are also more sensitive to predatory threats than other groups (McComb et al., 2011; McComb, Moss, Durant, Baker, & Sayialel, 2001). Hence, the death of such an experienced leader could have a long-lasting negative impact on group fitness due to the loss of knowledge. However, there are also episodic leaders (e.g. individuals that lead a group for a limited time because they have acquired information about the location of resources (Robson & Traniello, 2002) or are merely the hungriest individuals in their group (Krause, 1993)). In these cases, the benefits of individual leadership would be more ephemeral. Apart from leaders, catalysts, which facilitate group behaviour by stimulating task performance in other group members (Robson & Traniello, 1999), could also be described as a keystone role. For example, during house hunting in honey bee swarms, about 5% of all bees act as catalysts by performing a vibration signal that enhances liftoff preparations and swarm movement (Donahoe, Lewis, & Schneider, 2003).

Pioneers or Population Founders

Similar to organisms that act as foundational species or ecosystem engineers (Jones, Lawton, & Shachak, 1994), individual colonists have the potential to become keystone individuals for their subsequent populations if they shape the environment in ways that go beyond simply choosing the site that others join. In addition, colonists' genotypes will determine the genetic milieu that is available to descendant populations in the immediate future. In these ways, colonists (or 'pioneers') are predisposed to have a disproportionately large impact on the long-term viability of new populations. In the case of phenotypic-biased dispersal, pioneers may exhibit a specialized phenotype. For instance, dispersal morphs of many insects are far more likely to colonize novel habitat patches. However, perhaps equally as often, pioneers are merely a generic subset of individuals from their source population that by chance colonize a new habitat patch (e.g. a hurricane blowing a gravid butterfly to a new island). In mosquitofish, *Gambusia affinis*, the behaviour of colonist behavioural types engenders a social environment that facilitates the invasion of other behavioural tendencies. Asocial mosquitofish are intolerant of conspecifics, and thus, are more likely to disperse into new environments. However, asocial individuals actually facilitate the subsequent invasion of social individuals, via conspecific attraction (Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010). In other words, asocial individuals could be described as keystone individuals because they change the social environment in ways that allow social individuals to invade a new habitat.

Pioneers may also have important transgenerational effects because both the pioneer's traits and the environment that they create are effectively inherited by subsequent generations (similar to the pacific culture in primates: Sapolsky & Share, 2004). For instance, in the facultative social spider *Anelosimus studiosus*, the survival of entire lineages depends on the behavioural traits of population founders/progenitors. Subpopulations founded by docile individuals grow four times faster than other subpopulations, but also suffer increased susceptibility to natural enemies. Without immigration of aggressive individuals (i.e. genetic rescue effects), natural enemies quickly localize in on undefended, docile subpopulations and within two to four generations cause nine-fold increases in their extinction risk (Pruitt, 2013). In contrast, subpopulations founded by aggressive individuals or by a mixture of aggressive and docile individuals are far less susceptible to extinction.

The Bad Apple versus the Golden Fruit

Despite numerous examples where keystone individuals augment group performance, there are equally compelling cases where keystone individuals have disruptive effects on group performance. In troops of baboons, the immigration of highly aggressive males into new groups can lead to violent shifts in dominance hierarchies. These dynamics stress resident females and result in a high incidence of spontaneous abortions (Alberts et al., 1992). The hyperaggressiveness of select male water striders can have similarly adverse effects on group performance. In a typical day, male water striders spend approximately 30% of their time in copula. Much of their remaining time is spent attempting to court or coerce females of varying receptivity. In contrast to normal males, hyperaggressive males are so zealous in their mating behaviour that they rarely successfully mount females. Instead, hyperaggressive males spend the majority of their time waged in male–male or male–female agonistic disputes. In response, the majority of females (and males) cease mating and foraging entirely, and seek refuge along the water shore (Chang & Sih, 2013; Sih & Watters, 2005). Thus, the hyperaggressiveness of a few keystone males has the potential to sterilize entire groups of individuals. Likewise, one or a few keystone cheaters can so undermine a group that they cause societal collapse or group disbandment (Rankin, Bargum, & Kokko, 2007).

EVOLUTIONARY ORIGINS AND ECOLOGICAL CONSEQUENCES

Ecological Consequences

In this section we review some of the effects that keystone individuals can have on their social groups and briefly discuss the effects that keystone individuals could have on higher-order ecological phenomena.

Social groups

The ecological consequences of keystone individuals have been best characterized in context of social groups. In social animals, keystone individuals can influence virtually every aspect of groups' collective behaviour, ecology and success. First, leader individuals can permit their groups to make more accurate and informed decisions. For example, knowledgeable matriarchs can assist their groups to better avoid predators (McComb et al., 2011). Second, keystone individuals may also be instrumental in the transfer of valuable information. For example, informed scouts can help their colonies track high-quality and ephemeral food patches in complex landscapes. Or, knowledgeable tutors can generate a ripple effect that changes the course of cultural evolution for an entire population.

Although there are numerous studies that document the presence and effects of keystone roles in social settings, there exist many frontiers for further research. Two of the many outstanding challenges for researchers in this field are to (1) gain a deeper mechanistic understanding of how individuals in keystone roles impact their groups (e.g. how they communicate their status, how they shift the behaviour/physiology of fellow group members), and (2) explore how environmental variation shifts the profitability (or cost) of different kinds of keystone individuals. These lines of questioning will be key for moving the field beyond a loose assemblage of case studies and lay the groundwork for a predictive theoretical framework.

Populations

Considerably less is known about how keystone individuals influence population vitals and dynamics (e.g. carrying capacity, stability, growth rate, range shifts). And, the limited numbers of empirical papers on this topic, again, cover only social species. Thus, whether and how keystone individuals emerge in less socially integrated populations remains elusive, but not unlikely.

In the case of range fronts, pioneer individuals are powerful because their genes determine the starting gene pool for new populations. And, the environments that they engender can accelerate, halt or reverse population growth. Such population vitals are crucial for the persistence of incipient populations. In extreme cases, pioneers may facilitate the creation of superabundant and highly competitive populations of plants or animals that dominate over entire landscapes (e.g. ‘superclones’: Harrison & Mondor, 2011). At the other extreme, founders may set their populations on a course for inevitable extinction (Pruitt, 2013). Individuals or phenotypes with a greater propensity to disperse are more likely to serve as the pioneer phenotypes for new populations (Cote et al., 2010). In these cases, it is plausible that particular genotypes/phenotypes could actually evolve to specialize on the initial steps of colonization or invasion.

Whether or how keystone individuals shape other population characteristics, like populations stability or persistence, is less clear. However, the numerous costs/benefits that keystone individuals can have on social groups (Table 1) indicate that keystones could cause increases or decreases in population size, growth rates or carrying capacity. Additionally, keystone individuals that act as gateways between subpopulations could plausibly impact any population characteristic that is affected by population connectivity (e.g. rescue effects, source/sink dynamics, species' extinction risk). Although intuition suggests that keystone individuals can play an important role in population ecology, at present, there are only a few studies that have attempted to explore the effect of keystone individuals on general population-level processes. However, the results of these few studies have been promising.

Communities: keystone individuals versus keystone species

Here we examine the idea that there are synergisms between the concepts of keystone species (Paine, 1969) and keystone individuals. Keystone individuals may help to enhance the importance of keystone species, and keystone species may be a promising place to look for keystone individuals that influence overall community dynamics. In fact, one plausible reason why keystone species have such large effects is that they exhibit considerable intraspecific variation in key functional traits, like behaviour. If they do, then this opens the door for the possibility of disproportionalities among individuals in the strength of their influence. Consistent with this hypothesis, at least two studies on textbook examples of keystone species (California sea otters, *Enhydra lutris nereis*, and ochre sea stars, *Pisaster ochraceus*) have documented intraspecific variation in behaviour per se, and linked it to variation in resource utilization (Tinker, Bentall, & Estes, 2008) and predator effects on prey assemblages (Pruitt, Stachowicz, & Sih, 2012).

One of the greatest challenges for testing the effects of keystone individuals on biological communities is knowing where to start looking for them. Arguably, ecosystem engineers, foundation species, habitat forming species, keystone species and any species with large effects on their communities represent the most promising starting candidates for exploring the community-level effects of keystone individuals. In these species, the idiosyncratic behaviour of a single individual could have cascading or ricocheting effects to lower or higher trophic levels. In an illustrative case study, the idiosyncratic foraging forays of a pair of orcas eliminated the presence of rival predators for months, thus freeing lower trophic levels from their primary predators. In this situation, the orcas attacked and partially consumed a great white shark, *Carcharodon carcharias*, and uneaten components remained in the water for several days. This single foraging foray resulted in a mass dispersal of great white sharks out of the vicinity for several months (Pyle, Schramm, Keiper, & Anderson, 1999). In contrast, prior to the event and in previous years, white shark sightings were very common. It is unknown whether this was a case of competitive displacement or predator avoidance, but it remains of significant interest as it highlights how the interactions of a minority of individuals can drive large-scale ecological patterns.

Evolutionary Origins

In this section we discuss two general mechanisms to explain the emergence of keystone individuals: (1) keystone individuals are the product of genetic elements (i.e. keystone-conferring genotypes) that evolve under Darwinian selection and are therefore the product of selective forces on the keystones themselves; (2) keystone individuals are an experiential, state-dependent, or context-dependent phenomenon.

Maintenance of keystone-conferring genotypes

We reason here that illuminating how keystone individuals come to be and characterizing the performance consequences that they have on fellow group members is key to a deeper understanding of how societies evolve and function. In this first section, we will consider how keystone genotypes might evolve, and we offer several factors that could (1) help maintain keystone-conferring genotypes within mixed populations and (2) exaggerate, diminish or extinguish the large effects that keystone individuals exert on their groups.

The maintenance of keystone-conferring genotypes in a population is perhaps easiest to explain with environmental contingencies. Even if an individual is predisposed to become a keystone individual because it possess a certain genotype, the interaction between phenotype and social/physical environment will determine (a) whether an individual will be a keystone or not, (b) whether being a keystone is profitable and (c) whether the keystone individual will be beneficial or costly for the group. In a hypothetical example, consider a situation where a keystone individual obtains the majority of some profitable and defensible resource, for instance, by guarding and regulating access to a limited number of fruit-bearing trees. In these circumstances, the degree to which keystone individuals enjoy an advantage (or a disadvantage) could differ depending on the year's productivity: in normal years, the keystone individual may acquire more resources than other individuals, but, in years of extremely low or extremely high productivity, the keystone individual may have no fruit to defend at all, or there is so much fruit that the resource becomes indefensible. Thus, variation in resource availability can weaken or strengthen the effect that keystone individuals have on their groups and the relative benefit (or cost) of being a keystone. This, in turn, may help to maintain genotypic richness within populations. Social context and experience add another layer of complexity and contingency to the genotype–phenotype relationship. For instance, individuals' relationships with coalition mates, recent nutritional intake, history of injury/disease and any number of other factors could bias keystone-conferring genotypes against becoming a keystone, or alternatively, could allow genotypes that would not normally become a keystone individual to vault into the position. This layer of environmental contingencies, when integrated across time, effectively weakens selection on underlying genotypes.

Negative frequency-dependent selection is another familiar mechanism by which intra-and interspecific variation can be maintained. Negative frequency-dependent selection occurs when a phenotype/genotype experiences a fitness advantage when rare but becomes progressively disadvantaged as it increases in frequency. Negative frequency-dependent selection could be important in the maintenance of keystone-conferring genotypes: first, because it can prevent both keystone-conferring genotypes and generic genotypes from proceeding to fixation, and second, because the rates at which the fitness of genotypes decay as they increase/decrease in frequency will determine the stable mixture of genotypes within the population. Frequency-dependent effects of keystone individuals have been documented in some systems, which lend some support for the importance of this mechanism. For instance, the presence of a single group leader, or a small number of leaders, is beneficial to group movement and a host of subsequent group behaviours (Couzin, Krause, Franks, & Levin, 2005; Johnstone & Manica, 2011). This is because intragroup conflict will increase and decision-making speed will decrease if the frequency of leaders increases beyond a certain threshold. Groups that exhibit the optimal composition of keystone and nonkeystone phenotypes are predicted to enjoy superior performance. Therefore, there may be an optimal ratio of keystone versus nonkeystone individuals in a group (Smith & Price, 1973). This differential performance and survival of social groups may even lay the groundwork for interdemic selection to hone the optimal keystone/nonkeystone ratio (Levin & Kilmer, 1974).

Social heterosis is another mode by which keystone-conferring genotypes could be maintained alongside nonkeystone genotypes within a population. Social heterosis describes the maintenance of genotypic diversity (i.e. keystone and nonkeystone genotypes) via mutualistic interactions between behaviourally diverse individuals within groups (Nonacs & Kapheim, 2007). The theory of social heterosis is particularly useful in that it explains group genetic diversity without invoking frequency dependence, antagonistic pleiotropy, migration, or any other explanation required in alternative theoretical frameworks, and is thus a concise and parsimonious theory (Nonacs & Kapheim, 2007). The theory argues that, in spatially structured populations, demes/groups composed of unlike genotypes will outperform homogenous groups. Thus, over time, heterogeneous groups are predicted to outlive and replace homogenous groups within the population. No single genotype is permitted to increase to fixation because, as it does, the remaining heterogeneous groups will experience ever-increasing relative performance, and thereby outcompete homogeneous groups. This mechanism operates just like within-individual heterosis in hybrid solitary organisms, except the positive interactions among alleles play out among individuals in structured subpopulations. Modelling efforts have demonstrated that these dynamics have the potential to maintain genotypic diversity within populations (Nonacs & Kapheim, 2007). A limited but growing number of empirical tests have recovered support for this theory's predictions, as groups that contain a diverse mixture of behavioural types tend to outperform monotypic groups (Modlmeier & Foitzik, 2011; Modlmeier, Liebmann, & Foitzik, 2012; Pruitt & Riechert, 2011).

We argue that the effect (positive versus negative) that keystone-conferring genotypes have on their group will set the stage for coevolution between keystone and nonkeystone genotypes, which in turn, will have cascading effects on the evolutionary stability and effect size of keystone individuals. Intraspecific coevolution occurs among interacting phenotypes within a population along a spectrum of mutualism (e.g. cooperative foraging: Wenzel & Pickering, 1991) to antagonism (e.g. sexual conflict: Arnqvist & Rowe, 2002). We reason that cooperative coevolution may augment the impact of keystone individuals on their group and enhance the fitness interests of one or both phenotypes. In cases where keystone individuals have a positive impact on other group members, selection should favour traits in nonkeystone individuals that augment the effect of keystone individuals. For example, in social insects, the success of queens is contingent on the cooperation of worker individuals. In these systems, the utility of keystone individuals (i.e. queens) is so intimately tied to the contributions of nonkeystone individuals (i.e. workers) that neither phenotype has utility without the other. As it happens, the idea that worker phenotypes have evolved to accentuate the performance of keystone reproductives is 'the' prevailing hypothesis for how eusociality has evolved (Oster & Wilson, 1979). Under such mutualistic scenarios, we would expect the effect of keystone individuals on their groups to become more accentuated over evolutionary time. Alternatively, when keystone phenotypes depress the fitness of nonkeystones, antagonistic coevolution between keystones and nonkeystones may slow, halt or reverse the evolution of keystone individuals. Under such circumstances, evolution should favour traits in keystone individuals that accentuate the effects they have on nonkeystones, to the extent that it benefits the keystone individual itself. However, evolution should favour traits in nonkeystones that diminish the keystone's effects. All things being equal, the collective population size and mutation rate of the population of nonkeystones should be far greater than in keystone individuals. Thus, nonkeystones are predicted to 'win' such antagonistic arms races. The resulting prediction is that the effects of keystones should diminish over time, and thus, their persistence should be only ephemeral.

Experience, and state and context dependence

Experience, particularly early in life, has the potential to bias individuals' propensity to assume keystone roles, particularly where there is a positive feedback loop between individuals' experiences, their success and the influence they ultimately wield over their groups. For example, prosperous experience in tasks like resource discovery can result in inordinate proficiency and/or specialization relative to other group members (e.g. informed leaders govern resource finding in fish schools: Reebs, 2000). Furthermore, an experienced individual may sometimes monopolize a limited resource and enjoy an augmented growth rate and body condition which, in turn, allows that individual to maintain persistent control over said resources. This positive feedback loop, which has been observed in feeding dominance hierarchies in rainbow trout, *Oncorhynchus mykiss* (McCarthy, Carter, & Houlihan, 1992), highlights one process by which an occupant of a keystone role can uphold its status (seemingly) indefinitely. Similarly, individuals that hold experientially determined dominant roles can hoard potential mates (e.g. elephant seals, *Mirounga augustirostris*: Le Boeuf, 1974) and can broker the access of subordinate individuals to mating opportunities (Frank, 1986). In these cases, a keystone individual can arise via circumstances in earlier life, and the influence of these individuals is further accelerated by the spoils of being a dominant individual (i.e. a positive feedback loop).

In some cases, keystone individuals may arise only under certain circumstances (i.e. context dependence) or only when a certain physiological state is achieved (i.e. state dependence). State-dependent phenotypes may be governed by several mechanisms, such as: (1) differential gene expression between individuals due to resource acquisition (e.g. royal jelly in *Apis mellifera*; Corona, Estrada, & Zurita, 1999), (2) the strength with which a keystone individual's hormonal state exerts an influence on other group members (e.g. lactation in plains zebra, *Equus burchellii*: Fischhoff et al., 2007), or (3) high neuroendocrine activity (e.g. basal cortisol and testosterone levels in primates; Alberts et al., 1992). Hormones are presumed to be a major mechanism coordinating interactions between different individuals (Adkins-Regan, 2005). Hence, hormones should play a key role in regulating whether or not an individual will inhabit a keystone role. For instance, testosterone and juvenile hormone represent potentially crucial mechanisms in establishing the dominance status of an individual. In male chacma baboons, *Papio hamadryas ursinus*, present testosterone levels can predict future dominance rank (Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2006). Similarly, juvenile hormone has been shown to be a decisive factor in rank establishment in lobster cockroaches, *Nauphoeta cinerea* (Kou, Chou, Chen, & Huang, 2009). In contrast, high levels of serotonin are indicative of submissive behaviour and can even lead to a reverse of dominant social status (e.g. *Anolis carolinensis* lizards; Larson & Summers, 2001). Once dominance is established, individuals could use pheromones to communicate and maintain their status via honest signalling (e.g. social wasps; van Zweden, Bonckaert, Wenseleers, & d'Ettorre, 2013). The physiological requirements of inhabiting and maintaining a keystone role could then determine whether a keystone role can be occupied by generic individuals or only keystone individuals. Episodic keystone individuals may express the appropriate levels of hormones only during critical periods so as to reduce costs of consistently high expression levels (e.g. the challenge hypothesis: Wingfield, Hegner, Dufty, & Ball, 1990). An individual's current condition (i.e. sickness, disease, injury) can also increase the risk of predator attack on the whole group by alerting predators to their presence (Krause & Ruxton, 2002). Even though the focal sick animal is most at risk to predation or parasitism, high group viscosity can distribute the risk of mortality to nonkeystones. Consequently, there is a nearly limitless set of combinations of experience, state and context that could magnify an episodic keystone's effect on group dynamics and survival.

CONCLUSIONS AND FUTURE DIRECTIONS

We present herein a unifying framework that can be used to study the evolutionary and ecological implications of keystone individuals across various test systems. Grounded in the keystone species concept, we offer a general terminology that defines keystone individuals as individuals that have a disproportionally large influence on other group members or group dynamics relative to their abundance. We also provide subcategories (i.e. episodic and fixed) of keystone individuals, describing the regularity of their effects on the group. We believe that the generality of this terminology will allow researchers to develop ideas across species boundaries and to explore and compare commonality in evolutionary and ecological patterns. In particular, we hope that our synthesis of the existing literature will instigate researchers to consider the significance of keystone individuals in their test systems. Keystone individuals are not only widespread in animal groups, but also highly diverse in the roles they occupy. Alpha individuals, leaders, control animals and superspreaders are only some of the most prominent examples for the diversity of keystone roles that can be found in the existing literature. Ignoring their presence through oversights or mischaracterizations could not only lead to false conclusions and impede conservation efforts (Williams & Lusseau, 2006) but, in the worst case, cost lives (e.g. superspreaders: Meyers et al., 2005).

We provide some practical methodological approaches that can be used to identify potential keystone individuals, distinguish between true, irreplaceable keystone individuals and generic individuals, and most importantly, measure their effect on group dynamics. Concerning the ecological implications and evolutionary origins of keystone individuals, we have identified various exciting opportunities for empirical and theoretical advancement and suggest unchartered frontiers that could give new insights on the evolution of not only keystone individuals, but of sociality in general. In particular, future studies should strive to gain a deeper understanding of how keystone individuals impact the behaviour and physiology of other group members and how these traits mediate group dynamics. Another promising direction is exploring how social and asocial environmental variation shifts the profitability (or costs) of keystone individuals on their group or community. Finally, we hope that our unifying framework, ideas and methodological approaches will inspire researchers to empirically test some of the hypotheses presented herein and further discover general evolutionary and ecological patterns.

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Supplementary Material

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References

Adkins-Regan, E. (2005). *Hormones and animal social behavior*. Princeton, NJ, U.S.A.: Princeton University Press.

Alberts, S. C., Sapolsky, R. M., & Altmann, J. (1992). Behavioral, endocrine, and immunological correlates of immigration by an aggressive-male into a natural primate group. *Hormones and Behavior, 26*, 167–178.

Arnqvist, G., & Rowe, L. (2002). Antagonistic coevolution between the sexes in a group of insects. *Nature, 415*, 787–789.

Ballard, W. B., & Robel, R. J. (1974). Reproductive importance of dominant male greater-prairie chickens. *Auk, 91*, 75–85.

Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2006). Testosterone predicts future dominance rank and mating activity among male chacma baboons. *Behavioral Ecology and Sociobiology, 59*, 469–479.

Bernstein, I. S. (1966). Analysis of a key role in a capuchin (*Cebus albifrons*) group. *Tulane Studies in Zoology, 13*, 49–54.

Bernstein, I. S. (1969). Stability of the status hierarchy in a pigtail monkey group (*Macaca nemestrina*). *Animal Behaviour, 17*, 452–458.

Bolnick, D. I., Amarasekare, P., Araujo, M. S., Burger, R., Levine, J. M., Novak, M., et al. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution, 26*, 183–192.

Bolnick, D. I., Svanback, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., et al. (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist, 161*, 1–28.

Chang, A. T., & Sih, A. (2013). Multilevel selection and effects of keystone hyper-aggressive males on mating success and behavior in stream water striders. *Behavioral Ecology, 24*, 1166–1176.

Clarke, F. M., & Faulkes, C. G. (1997). Dominance and queen succession in captive colonies of the eusocial naked mole-rat, *Heterocephalus glaber*. *Proceedings of the Royal Society B, 264*, 993–1000.

Corona, M., Estrada, E., & Zurita, M. (1999). Differential expression of mitochondrial genes between queens and workers during caste determination in the honeybee *Apis mellifera*. *Journal of Experimental Biology, 202*, 929–938.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T., & Sih, A. (2010). Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society B, 277*, 1571–1579.

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature, 433*, 513–516.

Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecology Letters, 15*, 1189–1198.

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters, 7*, 734–739.

Donahoe, K., Lewis, L. A., & Schneider, S. S. (2003). The role of the vibration signal in the house-hunting process of honey bee (*Apis mellifera*) swarms. *Behavioral Ecology and Sociobiology, 54*, 593–600.

Dornhaus, A., Holley, J.-A., Pook, V. G., Worswick, G., & Franks, N. R. (2008). Why do not all workers work? Colony size and workload during emigrations in the ant *Temnothorax albipennis*. *Behavioral Ecology and Sociobiology, 63*, 43–51.

Drews, C. (1993). The concept and definition of dominance in animal behavior. *Behaviour, 125*, 283–313.

Fischhoff, I. R., Sundaresan, S. R., Cordingley, J., Larkin, H. M., Sellier, M.-J., & Rubenstein, D. I. (2007). Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Animal Behaviour, 73*, 825–831.

Flack, J. C., Girvan, M., de Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature, 439*, 426–429.

Flack, J. C., Krakauer, D. C., & de Waal, F. B. M. (2005). Robustness mechanisms in primate societies: a perturbation study. *Proceedings of the Royal Society B, 272*, 1091–1099.

Frank, L. G. (1986). Social organization of the spotted hyaena *Crocuta crocuta*. II. Dominance and reproduction. *Animal Behaviour, 34*, 1510–1527.

Harrison, J. S., & Mondor, E. B. (2011). Evidence for an invasive aphid ‘superclone’: extremely low genetic diversity in oleander aphid (*Aphis nerii*) populations in the southern United States. *PLoS One, 6*, e17524.

Johnstone, R. A., & Manica, A. (2011). Evolution of personality differences in leadership. *Proceedings of the National Academy of Sciences of the United States of America, 108*, 8373–8378.

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos, 69*, 373–386.

Knörnschild, M., Nagy, M., Metz, M., Mayer, F., & von Helversen, O. (2010). Complex vocal imitation during ontogeny in a bat. *Biology Letters, 6*, 156–159.

Kou, R., Chou, S.-Y., Chen, S.-C., & Huang, Z. Y. (2009). Juvenile hormone and the ontogeny of cockroach aggression. *Hormones and Behavior, 56*, 332–338.

Krause, J. (1993). The relationship between foraging and shoal position in a mixed shoal of roach (*Rutilus rutilus*) and chub (*Leuciscus cephalus*): a field study. *Oecologia, 93*, 356–359.

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford, U.K.: Oxford University Press.

Larson, E. T., & Summers, C. H. (2001). Serotonin reverses dominant social status. *Behavioural Brain Research, 121*, 95–102.

Le Boeuf, B. J. (1974). Male–male competition and reproductive success in elephant seals. *American Zoologist, 14*, 163–176.

Levin, B. R., & Kilmer, W. L. (1974). Interdemic selection and the evolution of altruism: a computer simulation study. *Evolution, 28*, 527–545.

Lusseau, D., & Newman, M. E. J. (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society B, Supplement, 271*, S477–S481.

McCarthy, I. D., Carter, C. G., & Houlihan, D. F. (1992). The effect of feeding hierarchy on individual variability in daily feeding of rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Journal of Fish Biology, 41*, 257–263.

McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. *Science, 292*, 491–494.

McComb, K., Shannon, G., Durant, S. M., Sayialel, K., Slotow, R., Poole, J., et al. (2011). Leadership in elephants: the adaptive value of age. *Proceedings of the Royal Society B, 278*, 3270–3276.

Meyers, L. A., Pourbohloul, B., Newman, M. E. J., Skowronski, D. M., & Brunham, R. C. (2005). Network theory and SARS: predicting outbreak diversity. *Journal of Theoretical Biology, 232*, 71–81.

Mills, L. S., Soule, M. E., & Doak, D. F. (1993). The keystone-species concept in ecology and conservation. *Bioscience, 43*, 219–224.

Modlmeier, A. P., & Foitzik, S. (2011). Productivity increases with variation in aggression among group members in *Temnothorax* ants. *Behavioral Ecology, 22*, 1026–1032.

Modlmeier, A. P., Liebmann, J. E., & Foitzik, S. (2012). Diverse societies are more productive: a lesson from ants. *Proceedings of the Royal Society B, 279*, 2142–2150.

Naug, D. (2008). Structure of the social network and its influence on transmission dynamics in a honeybee colony. *Behavioral Ecology and Sociobiology, 62*, 1719–1725.

Nonacs, P., & Kapheim, K. M. (2007). Social heterosis and the maintenance of genetic diversity. *Journal of Evolutionary Biology, 20*, 2253–2265.

Oster, G. F., & Wilson, E. O. (1979). *Caste and ecology in the social insects*. Princeton, NJ, U.S.A.: Princeton University Press.

Paine, R. T. (1969). A note on trophic complexity and community stability. *American Naturalist, 103*, 91–93.

Paine, R. T. (1995). A conversation on refining the concept of keystone species. *Conservation Biology, 9*, 962–964.

Paull, S. H., Song, S., McClure, K. M., Sackett, L. C., Kilpatrick, A. M., & Johnson, P. T. J. (2011). From superspreaders to disease hotspots: linking transmission across hosts and space. *Frontiers in Ecology and the Environment, 10*, 75–82.

Pinter-Wollman, N., Hubler, J., Holley, J. A., Franks, N. R., & Dornhaus, A. (2012). How is activity distributed among and within tasks in *Temnothorax* ants? *Behavioral Ecology and Sociobiology, 66*, 1407–1420.

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., et al. (1996). Challenges in the quest for keystones. *Bioscience, 46*, 609–620.

Pruitt, J. N. (2013). A real-time eco-evolutionary dead-end strategy is mediated by the traits of lineage progenitors and interactions with colony invaders. *Ecology Letters, 16*, 879–886.

Pruitt, J. N., & Riechert, S. E. (2011). How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proceedings of the Royal Society B, 278*, 1209–1215.

Pruitt, J. N., Stachowicz, J. J., & Sih, A. (2012). Behavioral types of predator and prey jointly determine prey survival: potential implications for the maintenance of within-species behavioral variation. *American Naturalist, 179*, 217–227.

Pyle, P., Schramm, M. J., Keiper, C., & Anderson, S. D. (1999). Predation on a white shark (*Carcharodon carcharias*) by a killer whale (*Orcinus orca*) and a possible case of competitive displacement. *Marine Mammal Science, 15*, 563–568.

Rankin, D. J., Bargum, K., & Kokko, H. (2007). The tragedy of the commons in evolutionary biology. *Trends in Ecology & Evolution, 22*, 643–651.

Reebs, S. G. (2000). Can a minority of informed leaders determine the foraging movements of a fish shoal? *Animal Behaviour, 59*, 403–409.

Robson, S. K., & Traniello, J. F. A. (1999). Key individuals and the organization of labor in ants. In C. Detrain, J. L. Deneubourg, & J. Pasteels (Eds.), *Information processing in social insects* (pp. 239–259). Basel, Switzerland: Birkhäuser Verlag.

Robson, S. K., & Traniello, J. F. (2002). Transient division of labor and behavioral specialization in the ant *Formica schaufussi*. *Naturwissenschaften, 89*, 128–131.

Sapolsky, R. M., & Share, L. J. (2004). A pacific culture among wild baboons: its emergence and transmission. *PLoS Biology, 2*, E106.

Seeley, T. D., Morse, R. A., & Visscher, P. K. (1979). The natural history of the flight of honey bee swarms. *Psyche, 86*, 103–113.

Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters, 15*, 278–289.

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology, 63*, 975–988.

Sih, A., & Watters, J. V. (2005). The mix matters: behavioural types and group dynamics in water striders. *Behaviour, 142*, 1417–1431.

Smith, J. M., & Price, G. (1973). The logic of animal conflict. *Nature, 246*, 15.

Stroeymeyt, N., Franks, N. R., & Giurfa, M. (2011). Knowledgeable individuals lead collective decisions in ants. *Journal of Experimental Biology, 214*, 3046–3054.

Tinker, M. T., Bentall, G., & Estes, J. A. (2008). Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 560–565.

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., et al. (2012). The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution, 27*, 244–252.

Vital, C., & Martins, E. P. (2011). Strain differences in zebrafish (*Danio rerio*) social roles and their impact on group task performance. *Journal of Comparative Psychology, 125*, 278–285.

Vital, C., & Martins, E. P. (2013). Socially-central zebrafish influence group behavior more than those on the social periphery. *PLoS One, 8*, e55503, http://dx.doi.org/10.1371/journal.pone.0055503.

Wenzel, J. W., & Pickering, J. (1991). Cooperative foraging, productivity, and the central limit theorem. *Proceedings of the National Academy of Sciences of the United States of America, 88*, 36–38.

Wey, T., Blumstein, D. T., Shen, W., & Jordan, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour, 75*, 333–344.

Williams, R., & Lusseau, D. (2006). A killer whale social network is vulnerable to targeted removals. *Biology Letters, 2*, 497–500.

Wingfield, J. C., Hegner, R. E., Dufty, A. M., Jr., & Ball, G. F. (1990). The 'challenge hypothesis': theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist, 136*, 829–846.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution, 27*, 452–461.

van Zweden, J. S., Bonckaert, W., Wenseleers, T., & d'Ettorre, P. (2013). Queen signalling in social wasps. *Evolution*. http://dx.doi.org/10.1111/evo.12314. Advance online publication.