Animal Behaviour 89 (2014) 53–62

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Review

The keystone individual concept: an ecological and evolutionary overview

Andreas P. Modlmeier [a,*], Carl N. Keiser [a], Jason V. Watters [b], Andy Sih [c], Jonathan N. Pruitt [a]

[a] Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, U.S.A.
[b] San Francisco Zoological Society, San Francisco, CA, U.S.A.
[c] Department of Environmental Science and Policy, University of California at Davis, CA, U.S.A.

ARTICLE INFO

Article history:
Received 19 September 2013
Initial acceptance 5 November 2013
Final acceptance 10 December 2013
Available online 17 January 2014
MS. number: ARV-13-00786R

Keywords:
collective decision making
dominance
group dynamics
keystone individual
pioneer
social behaviour
social network theory

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

* Correspondence and present address: A. P. Modlmeier, Department of Biological Sciences, University of Pittsburgh, 213 Clapp Hall, 4249 Fifth Avenue, Pittsburgh, PA 15260, U.S.A.
E-mail address: andreas.modlmeier@gmail.com (A. P. Modlmeier).

0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2013.12.020

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.