Why do animal groups matter for conservation and management?

Adriana A. Maldonado-Chaparro1 | Gloriana Chaverri2,3

1Departamento de Biología, Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia
2Sede del Sur, Universidad de Costa Rica, Golfito, Costa Rica
3Smithsonian Tropical Research Institute, Ancón, Panama

Correspondence
Adriana A. Maldonado-Chaparro,
Departamento de Biología, Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia.
Email: adriana.maldonado@urosario.edu.co
Gloriana Chaverri, Sede del Sur,
Universidad de Costa Rica, Alamedas, Golfito 60701, Costa Rica.
Email: gloriana.chaverri@ucr.ac.cr

Abstract
The internationally recognized levels of conservation, namely ecosystems, species, and genes, have thus far served as important guidelines to determine how national and international laws should protect nature. However, a far ignored aspect of a species’ life history in the legislation is its tendency to form social groups. Group members greatly depend on each other for survival and reproduction, and when the persistence of groups is threatened, so may the population as a whole. Humans affect groups through indirect activities, such as tourism, or directly by removing individuals through poaching, for example. These activities disturb groups in both predictable and unpredictable ways: destabilizing dominance hierarchies, changing the strength of social relationships, modifying cooperative interactions, reducing alloparental care, and altering social skills, among others. We propose that greater efforts must be undertaken first, to more thoroughly understand how our actions are affecting group dynamics in as many species as possible, and second, to adapt policies to reduce the negative effects of direct and indirect anthropogenic activities on group and population persistence.

Keywords
conservation policies, demography, disturbances, social structure, sociality

1 | INTRODUCTION

The main goal of conservation biology is to maintain the current global biological diversity and the diversification processes (Mace, 2003). Yet conservation policies traditionally focus on three primary levels of biological organization: ecosystem, species, and genes (Coates, Byrne, & Moritz, 2018). However, in considering solely these discrete levels we may be ignoring the importance of a fourth one, populations, which in group-living species have another level of variation related to their social dynamics. Thus, populations may nonetheless be critical for protecting the long-term survival of species and for maintaining ecosystem services (Luck, Daily, & Ehrlich, 2003). To ensure the persistence of populations and the evolutionary processes, conservation practitioners should rely on intermediate levels of organization that integrate biological variation below the species level (Mee, Bernatchez, Reist, Rogers, & Taylor, 2015). Here, we aim to highlight how our understanding of within population variation arising from the tendency of
animals to form social groups contributes to planning effective conservation and management strategies.

In many vertebrates, populations are structured in smaller components: the social groups, which consist of a set of individuals of different age, sex, and life histories that preferentially interact and associate with a given set of conspecifics and more so with each other than with other set of conspecifics (Alexander, 1974). Within a group, individuals exhibit a diversity of social, dispersal, and reproductive strategies that affect the genetic structure and the short and long-term dynamics of populations (Parreira & Chikhi, 2015). For example, differences in the structure and composition of killer whale (*Orcinus orca*) groups led to differences in population-level demographic parameters (Brault & Caswell, 1993), revealing the importance of group-dynamics on population persistence. Despite the ecological importance of sociality (Ward & Webster, 2016), groups and group-related traits have been largely overlooked within national and international legislation, and when planning conservation and management strategies.

To demonstrate the importance of groups within a population and conservation context, we first summarize the impact of sociality on demographic processes. Then, we explore the potential effects of human-caused disturbances to the dynamics of groups based on published studies and suggest other topics that should be addressed to strengthen our understanding of the potential effects of human-induced disturbances on animal groups. We also attempt to establish whether there is evidence for conservation policies that could help minimize the effects of human-caused disturbances to the dynamics of groups; based on our findings, we briefly discuss some conservation tools and actions that could easily be implemented to protect groups. We argue that incorporating the concept of groups into a conservation framework is necessary not only to strengthen the protection of social species, but also their behavioral diversity. Our goal is to provide a critical assessment of a hitherto aspect of species’ natural history that is lacking from conservation policies, but which may provide a powerful tool in our efforts to protect wildlife.

2 | DEMOGRAPHIC IMPORTANCE OF SOCIAL GROUPS

Populations do not consist of merely a pool of individuals that are independent from each other. Indeed, within a population, individuals can consistently interact and associate with only a subset of individuals, resulting in an underlying structure: the social group. In turn, group behavior emerges from the interaction of this subset of individuals. This has a twofold consequence. First, because groups are an evolutionary response to reduce predation risk and increase resource and information acquisition (Ward & Webster, 2016), then their dynamics are expected to influence the outcome of demographic processes such as survival, reproduction, and dispersal (e.g., Bateman, Ozgul, Nielsen, Coulson, & Clutton-Brock, 2013; Grimm et al., 2003). Second, because within groups there is variation in the pattern of social relationships among their members, individuals experience their social environment in different ways and thus we could expect the benefits and consequences of these relationships to also vary, which can lead to differences in vital rates (e.g., Formica et al., 2012; Silk et al., 2009). Therefore, sociality can have demographic consequences and thus can determine the dynamics of a population.

The social structure (i.e., the patterns of social relationships among individuals; Hinde, 1976) can affect demographic parameters (Brault & Caswell, 1993) and can also be affected by environmental disturbances. In face of disturbance events, individuals can adjust their behavioral and physiological responses or can alter their life-history traits. These changes can affect survival and mortality rates and thus influence the social organization and structure of the groups, and potentially resulting in an unstable state (i.e., social instability). For example, in species with dominance hierarchies, the death of a high-ranking individual can lead to an increase in the rate of aggressive interactions (e.g., Kaburu, Inowe, & Newton-Fisher, 2013) or to a temporal decrease in the cohesion of the group (e.g., Franz, Altmann, & Alberts, 2015). If the group cannot rapidly recover to its most adaptive state (i.e., highest mean individual fitness), it can negatively affect population dynamics leading to population decrease and eventual extinction.

It becomes notable that sociality plays a key role in driving population-level outcomes. However, there is little empirical evidence revealing the fitness consequences of environmental disturbance, especially in group-living species. Indeed, our current knowledge derives from evidence showing that disturbances can have negative effects on the social structure of the population (Table 1) and from studies showing that social relationships have fitness consequences (e.g., reviewed in Silk, 2014). This suggests that social dynamics are a fundamental aspect linking individual behavior to population-level outcomes. Thus, when formulating policies and planning conservation and management strategies, it would become fundamental to understand how to maintain the functionality of the groups that comprise the population, a plea echoed by other recent assessments (Brakes et al., 2021), but this is a big gap in the current literature.
| System Disruptor                                                                 | Effect                                                                                     | References                                                                 |
|---------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------|----------------------------------------------------------------------------|
| **Experimental manipulations**                                                   |                                                                                           |                                                                            |
| Vampire bats (*Desmodus rotundus*)                                               | Changes in group membership                                                               | Decrease propensity of food sharing                                      | Carter and Wilkinson (2013) |
| Degu (*Octodon degus*)                                                           | Changes in group membership                                                               | Decrease propensity of communal rearing                                   | Ebensperger et al. (2016)  |
| Bottlenose dolphins (*Tursiops spp.*)                                            | Removal of a key individual (simulation)                                                | Fragmentation of the community                                            | Lusseau and Newman (2004)  |
| Pigtailed macaques (*Macaca nemestrina*)                                         | Removal of a key individual                                                               | Disruption of policing and destabilization of social interactions         | Flack, Girvan, de Waal, and Krakauer (2006) |
| Great tits (*Parus major*)                                                        | Removal of focal individuals                                                              | Increased social connectivity between remaining individuals              | Firth et al. (2017)        |
| Zebra finches (*Taeniopygia guttata*)                                            | Repeated temporary splitting of the groups                                                | Decrease in the strength of social relationships and increase in the exclusivity of social relationships | Maldonado-Chaparro, Alarcón-Nieto, Klarevas-Irby, and Farine (2018) |
| Disc-winged bat (*Thyroptera tricolor*)                                          | Removal of roosting resources                                                             | Decrease in social cohesion                                               | Chaverri and Kunz (2011)   |
| **Natural disruptors**                                                            |                                                                                           |                                                                            |
| African striped mice (*Rhabdomys pumilio*)                                       | Drought                                                                                   | Switch from stable kin groups to instable non-kin groups                 | Schradin, Schubert, and Pillay (2006) |
| Toque macaques (*Macaca sinica*)                                                 | Cyclones and droughts                                                                     | Fragmentation of stable troops                                            | Dittus (1988)              |
| Tree lizard (*Urosaurus ornatus*)                                                | Burn frequency (change in habitat structure)                                             | Increased connections among individuals in frequently burned areas        | Lattanzio and Miles (2014) |
| Red-backed fairy-wren (*Malurus melanocephalus*)                                 | Wildfires (change in habitat structure)                                                   | Social cohesion among individuals in the remaining groups increased       | Lantz and Karubian (2017)  |
| Spotted dolphins (*Stenella frontalis*)                                          | High mortality due to a hurricane                                                         | Recruitment of individuals and increase in the cohesion of the subgroups  | Elliser and Herzing (2014) |
| **Antropogenic disruptors**                                                       |                                                                                           |                                                                            |
| Hyenas (*Crocuta crocuta*)                                                       | Proximity to human activity                                                              | Weaker social cohesiveness within clans that live in areas with more human activity and infrastructure | Belton, Cameron, and Dalerum (2018) |
| Longtailed macaques (*Macaca fascicularis*)                                      | Potential interactions with humans                                                        | Lower allogrooming frequency in individuals that monitored human activity more frequently | Marty et al. (2019)       |
| Giraffes (*Giraffa camelopardalis*)                                              | Proximity to human settlement                                                             | Weaker relationship strength in communities closer to humans             | Bond, König, Lee, Ozgul, and Farine (2020) |
| Audouin’s gull (*Larus audouinii*)                                               | Exposure to non-native predators                                                         | Decrease in social cohesion with when expose to predation                | Genovart et al. (2020)    |
| Bonnet macaques (*Macaca radiata*)                                               | Potential interactions with humans                                                        | Individuals that monitor more human activity show reduced grooming time and grooming partner diversity | Balasubramaniam et al. (2020) |

(Continues)
3 | DIRECT AND INDIRECT EFFECTS OF HUMAN-INDUCED DISTURBANCES ON ANIMAL GROUPS

Human activities can cause environmental disturbances which can directly or indirectly affect the social structure of the groups (Berger-Tal et al., 2011). Activities such as hunting directly affect the social dynamics of group members as they remove individuals from the group. For example, in African elephants (Loxodonta africana), social disruption resulting from culling or translocation events may alter social skills that are responsible for the maintenance of complex societies (Shannon et al., 2013). Similar effects have also been detected in tropical areas subject to poaching where the structure of the mixed-species flocks was disrupted as a result of animal extraction (Marthy & Farine, 2018). However, most evidence on the effects of environmental disturbances on social structure comes from simulations, experimental manipulations, and opportunistic catastrophic events (Table 1). For example, captive studies have shown that the loss of a key individual can disrupt the policing behavior, thus destabilizing the social structure and the dominance hierarchy of the group (Flack et al., 2006), while experiments in wild populations of great tits (Parus major) have shown that flock members increase the strength of their social relationships (i.e., group cohesiveness) in response to the loss of their associates (Firth et al., 2017). Finally, changes in group membership can also affect parental care and cooperative interactions that may influence individual survival. For example, in degus (Octodon degus), the propensity for nonrelated females to engage in alloparental care, and resulting offspring growth, decreases when group membership is disturbed (Ebensperger et al., 2017). These examples together indicate that disturbances can modify the social structure and can alter fitness-related traits, thus potentially affecting population dynamics.

Other activities, including tourism or habitat transformation, can also have disrupting consequences on social structure. On one hand, nonconsumptive activities such as hiking that seem to have less impact on the behavior of animals can affect social structure. Because hikers can be perceived as predators (Beale & Monaghan, 2004), such activities are known to elicit antipredator responses (Frid & Dill, 2002), thus triggering, among other behavioral responses, changes in group size and composition (e.g., Manor & Saltz, 2003). On the other hand, disturbances such as forest fragmentation modify the physical environment in which individuals move, thus influencing the probability of individuals to socially interact and thus their social dynamics (He, Maldonado-Chaparro, & Farine, 2019). These effects have been shown in red-backed fairywrens (Malurus melanopecephalus) where habitat loss from fire causes the population to become more densely connected (Lantz & Karubian, 2017). It has also been shown that in tourist areas giraffe populations have a loose social structure compared to those groups in more isolated areas (Muller, Cuthill, & Harris, 2019), and access to agroecosystems such as plantations can lead to increased aggression and decreased affiliation compared to groups in natural areas (e.g., forest; Holzner et al., 2020). Thus, permanent or temporary disturbances can directly or indirectly affect the way in which individuals interact (i.e., their social structure), and therefore can impact the survival and reproduction of individuals. These changes in the social dynamics can have long-term negative consequences for populations and should be an important consideration in managing wildlife populations.

4 | FUTURE DIRECTIONS FOR UNDERSTANDING THE IMPACT OF HUMAN DISTURBANCE ON GROUP AND POPULATION DYNAMICS

One important aspect that emerges clearly from the literature is that, for the majority of animal species, we still lack the most basic information about their social behavior, which then precludes us from even speculating about the effects of perturbations on group resilience and population persistence. We are now in the midst of rapid developments in technology (e.g., Argos and GPS satellite systems, ICARUS, bio-acoustic sensors, thermal imaging, miniaturized loggers) and analytic tools (e.g., deep learning, machine learning, neural networks) that are

Table 1 (Continued)

| System                  | Disruptor                          | Effect                                                                                           | References                                                                                   |
|-------------------------|------------------------------------|--------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------|
| Pigtailed macaques      | Access and use of palm plantations | Decreased affiliative interactions, and increased aggression. Loss of high dominant positions to low-ranking individuals. | Holzner, Balasubramaniam, and Ruppert (2020)                                                   |
allowing us to study groups in increasingly greater detail and in a wider range of species ranging from group-living to non-group-living (e.g., Abdul Mutalib, Ruppert, Kamaruszaman, Jamsari, & Nik Rosely, 2019; Allan et al., 2018; Browning et al., 2018; Burger, Fennessy, Fennessy, & Dierkes, 2020; Maekawa et al., 2020; Masmitja et al., 2020; Morita et al., 2021; Norouzzadeh et al., 2018; Ripperger et al., 2020; Teixeira, Maron, & Rensburg, 2019; Thorup et al., 2017; Wilber et al., 2019). These advances demonstrate a wide range of intra and interspecies variation and complexity of group dynamics, including non-group-living species. For example, GPS technology revealed that pumas (Puma concolor), a seemingly solitary species, exhibit a complex social structure that is affected by habitat fragmentation (Elbroch, Levy, Lubell, Quigley, & Caragiulo, 2017). This “cryptic” social structure has also been shown in other solitary species such as the slow loris (Nycticebus coucang) using radiotracking technology (Wiens & Zitzmann, 2003). Such variation in social complexity poses new challenges regarding the degree of generality of the effects of disturbances on group persistence. Below we propose a series of research topics that may help us close the gap between the social aspects of a species’ natural history and the effect of human-induced disturbances and move forward.

First, we need to understand the direct and indirect effects of removing individuals from groups and identify the costs borne from disturbances caused by anthropogenic activities. We have stated that the removal of key individuals (e.g., high-ranking) can have negative cascading effects on the social dynamics of the group (Flack et al., 2006) and on the structure of populations (Archie et al., 2008), but up to date it is not clear to what extent these effects can be generalized to other species. Additionally, dominance rank is just one of the social-related traits characterizing individuals. Within a group, members can also differ in the consistency of their behavior (i.e., personality traits), thus it is also important to strengthen our understanding of how personality affects the responses to anthropogenic disturbances. The effects of removing individuals from groups depend greatly on which behavioral types are targeted (Borg, Brainerd, Meier, & Prugh, 2015; Wolf & Weissing, 2012). In this sense, special measures regarding wildlife extraction must be taken to secure the survival of key group members (see Merrick & Koprowski, 2017), for example those that act as repositories of social information (Brakes et al., 2019, 2021).

Second, because harvest can disrupt the social structure of a population (Esteban et al., 2016), we can ask whether we should be removing individuals from smaller or larger groups or if we should remove single individuals from different groups or several individuals from the same group. In some cases, sociality can buffer the effects of environmental perturbations such that larger groups can be more resilient than smaller groups to the targeted removal of individuals. This is because larger groups have more redundant social connections and more opportunities to (re-) form new connections (Naug, 2009). To our knowledge, this question has not yet been addressed (but see Ausband, Mitchell, Stansbury, Stenglein, & Waits, 2017 for an example on how different hunting policies can affect group dynamics and offspring survival). However, what has been shown is that intense harvest can alter male mating patterns and decrease matriline persistence in a seemingly solitary-living species such as brown bears (Ursus arctos; Frank et al., 2020). Overall, what we are interested in understanding is how to ultimately maintain a group’s functionality, and thus the fitness of its individual components, despite the ever-increasing impacts of anthropogenic activities on natural systems.

A final thought closely related to ethical issues concerns a common debate among zoologists of whether the removal of individuals from natural populations for research purposes, for example during the collection of voucher specimens, is really justifiable (e.g., Russo, Ancillotto, Hughes, Galimberti, & Mori, 2017). Many animal populations are already struggling with a suite of human-caused conditions that have severely affected their long-term persistence, and many more will face similar fates. Therefore, we need to carefully consider whether additional losses are still sustainable or justifiable. There can be no doubt that museum collections, for example, have provided valuable data that inform conservation actions, such as the discovery of new species or long-term population trends, among many others (Patterson, 2001; Suarez & Tsutsui, 2004). However, during the process of collecting specimens we may be inadvertently affecting the stability of groups; therefore, collecting efforts may be decreasing population numbers beyond those that were initially intended. We hope that, by fostering further research on the effects of individual removal from groups and using this new understanding to direct conservation policies, we may be able to more effectively continue working towards the common goal of protecting wildlife.

5 Policies Regarding the Protection of Social Groups: Case Examples and Current Gaps

Despite the importance of social groups for individual survival and ultimately population persistence,
policymakers have not yet integrated social groups within the conservation and management framework. Additionally, they have not yet considered how disturbance to the groups may affect population persistence, which is reflected in wildlife extraction policies set forth by multiple governments. Costa Rica and Colombia, two megadiverse countries with strong policies regarding protection of wildlife, provide interesting examples of how extraction policies are mostly focused on the conservation of species or ecosystems, while still ignoring the importance of groups. We have chosen to present these two countries as an example given our familiarity with their conservation policies and our extensive experience conducting research on their native wildlife. While we cannot attest to the generalization of our findings, nor is it our goal to test this, we suspect the majority of countries similarly lack extraction policies that take an animal’s social behavior into account.

In both countries, there is no set number of individuals that is allowed to be removed for commercial (animal breeding farms) or noncommercial purposes (research or museum collections), but in general collecting charismatic, poorly known, or endemic species is usually not allowed. Similarly, other countries such as China, Chile, and Uruguay, among others, primarily protect rare, endangered, and/or economically important species, and there seems to be a general worldwide trend in prioritizing the conservation of charismatic species (Cirelli, 2002; Rees, 2017). In Costa Rica, each conservation area, which manages a number of protected areas in a region within the country, may establish a number of individuals that could be removed, and this number often depends on the ecosystem in question. In Colombia, wildlife extraction for different purposes is allowed under a license, except for subsistence hunting. However, despite the fact that the norm establishes that the administrative authorities of each region should regulate this practice, the number of individuals is not yet fully regulated. Extraction policies take population size and trends, reflected in a species’ conservation status, into consideration when granting permits for voucher collection. A species’ behavior, including its propensity to form groups, is not explicitly mentioned in any law or bylaws nor is it used, or even considered, by permit-granting authorities in these two countries as a criterion for restricting or regulating its extraction. Considering species’ social behavior in wildlife extraction policies appears to be similarly ignored in other countries’ legislation, such as Brazil, Bulgaria, Philippines, Malaysia, and South Africa. This may be similarly ignored in the legislation of most countries, but we were only able to extract the relevant information regarding access to biological resources for those few examples.

The previous examples show that governments have not yet considered how removing animals from their environments may affect the dynamics of groups and, in the long run, the dynamics of the populations they seek to protect. In Colombia there is one study that attempted to integrate social behavior to population management models (Maldonado-Chaparro & Blumstein, 2008). Although the results show that populations can recover from the consequences of removing a key individual (i.e., a dominant male), the exercise was theoretical and empirical evidence is needed to properly evaluate the extent of the effect. What is clear from many studies is that population resilience to, and recovery from, harvesting cannot be fully guaranteed despite a species’ seemingly ideal life history traits without considering also its social behavior (Wade, Reeves, & Mesnick, 2012).

6 | RECOMMENDED CONSERVATION TOOLS AND ACTIONS

As we continue to gather information that will answer some of the questions posed above to provide us with better tools to establish strong evidence-based policies, we may start implementing some simple changes to minimize our ever-increasing negative effects on group-living species. A relatively straightforward solution is to incorporate issues of animal welfare into the legislation. As pointed out by others, animal welfare is still a topic that is missing from laws pertaining the protection of biodiversity (Futhazar, 2020). One important component of animal welfare is maintenance of undisturbed group interactions, as noted in our previous sections, and thus should be considered relevant when governments grant permits for wildlife extraction. Clearly, this is a topic that has been considered relevant for social zoo or farm animals, which are required by law to be maintained within their groups (Rees, 2017); similar policies should be adopted for wild animals. Another important change that we propose is to provide rigorous protection of sites where group-living animals meet and strengthen their social bonds. In bats, for example, many social interactions occur almost exclusively at their roosting sites, such as caves, hollow trees, and many other structures (Kerth, 2008); by saving these sites, we are also protecting their social bonds (Chaverri & Kunz, 2011). Finally, governments should establish research priorities for social species that are constantly being harvested (legally or illegally); this way we can quickly make informed decisions to secure their continuous extraction (if this is desired) while providing the best possible protection of their populations.
7 | CONCLUDING REMARKS

In summary, although the extent to which anthropogenic disturbances affect social dynamics and how this feeds back into population-level processes is not well established, we have shown that anthropogenic disturbances can affect social dynamics and that the interactions happening at the group-level can determine demographic parameters such as survival and reproduction. It is clear that more evidence is needed in order to fully incorporate the protection of social species beyond the currently stipulated by national and international laws and bylaws. Given the large role of sociality for demographic processes, securing the persistence of healthy groups could strengthen the protection of populations and species. The conservation of the population's social structure may also be critical for the maintenance of behavioral diversity. Mounting evidence demonstrates that many behaviors are socially acquired (Brakes et al., 2021; Heyes & Galef Jr., 1996; Ramsey, 2013). Thus, the loss of groups, or their severe disruption, could prompt the loss of behavioral diversity (Kühl et al., 2019) and may result in a reduction of adaptability to changing conditions (Keith & Bull, 2017). Because of this, our main goal is to bring to the table this important aspect of the natural history of many species that has so far been neglected by conservation policies and permit-granting authorities, and to contribute to the further development of suitable strategies to conserve and manage wildlife.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

ORCID

Adriana A. Maldonado-Chaparro https://orcid.org/0000-0003-0853-4966
Gloriana Chaverri https://orcid.org/0000-0002-1155-432X

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