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The effects of human-caused mortality on mammalian cooperative breeders: a synthesis

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ABSTRACT

Human-caused mortality can be pervasive and even highly selective for individuals in groups of cooperative breeders. Many studies of cooperative breeders, however, do not address human-caused mortality. Similarly, studies focused on the effects of human-caused mortality on wildlife populations often do not consider the ecology of cooperative breeders. We searched the literature and identified 58 studies where human-caused mortality affected a group characteristic, vital rate, or population state of a cooperative breeder. Of studies reporting population growth or decline, 80% reported a link between human-caused mortality and population declines in cooperative breeders. Such studies often did not identify the mechanism behind population declines, but 28% identified concurrent declines in adult survival and another 21% reported concurrent declines in recruitment or reproduction. There was little overlap between the cooperative breeding and human-caused mortality literatures, limiting our ability to accrue knowledge. Future work would be beneficial if it (*i*) identified the vital rate(s) causing population declines, (*ii*) leveraged management actions such as lethal removal to ask questions about the ecology of group-living in cooperative breeders, and (*iii*) used insights from cooperative breeding theory to inform management actions and conservation of group-living species.

Key words: cooperative breeding, groups, harvest, mortality, poaching.

CONTENTS

I. INTRODUCTION

Cooperative breeding generally refers to animals who live and breed in groups where non-breeding individuals help care for the breeders' offspring. The fitness of individuals in such groups can increase with group size (Clutton-Brock, 2006; Gusset & Macdonald, 2010). Additionally, non-breeding individuals in groups of cooperative breeders can have increased access to food resources and ultimately higher survival as group size increases (Courchamp, Grenfell & Clutton-Brock, 1999*b*). Non-breeding individuals in groups are often offspring of the breeders and help to rear young. If young are related to the non-breeders, selection can favour such helping behaviour (Hamilton, 1964).

Large group size has consistently been associated with increased group success in cooperative breeders (Courchamp

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et al., 1999*b*; Courchamp, Rasmussen & Macdonald, 2002), although there can be an optimum group size that balances the benefits of large size with the costs of sharing limited food resources among group members (Creel & Creel, 1995). The success of groups of cooperative breeders, however, is not only contingent on group size. Even subtle changes to group composition can have marked effects on remaining group members. For example, losing older females in groups of African elephants (*Loxodonta africana*) led to lower reproductive rates for the remaining reproductively prime-aged females (Gobush, Mutayoba & Wasser, 2008). While breeder loss can be particularly influential in groups of cooperative breeders (Brainerd *et al.*, 2008), loss of non-breeding helpers can also negatively affect groups through lower survival of young (Courchamp, Clutton-Brock & Grenfell, 1999*a*; Courchamp & Macdonald, 2001).

Humans can negatively impact wildlife populations through direct mortality or by altering habitats and changing important behaviours (Milner, Nilsen & Andreassen, 2007). Human-caused mortality can be a dominant force influencing species declines around the globe, including populations of cooperative breeders (Finn, Grattarola & Pincheira-Donoso, 2023). Not all human-caused mortality leads to population declines, however. Many species can compensate for human-caused mortality through increases in other vital rates such as reproduction or even, at the population level, increased immigration rates (Adams *et al.*, 2008). For species where human-caused mortality is additive, populations can decline swiftly (Sparkman, Waits & Murray, 2011).

We might expect human-caused mortality to be particularly influential in populations of cooperative breeders due to the hierarchical nature of groups and the importance of group size and composition. Indeed, human-caused mortality is additive in some populations of cooperative breeders (Sparkman *et al.*, 2011). Furthermore, we might expect the effects of human-caused mortality to differ from natural mortality. For example, humans can be quite selective when removing individuals from groups leading to a cascade of negative effects due to changes in behaviours and mating structures in the surviving individuals (Packer & Pusey, 1983). While we know a great deal about the general ecology of cooperative breeders, many are not subject to persistent human-caused mortality (Koenig & Dickinson, 2016). Additionally, many studies that report on the effects of human-caused mortality have not done so through the lens of cooperative breeding (Collins & Kays, 2011; Hill, DeVault & Belant, 2019). Thus, we have a gap in knowledge where studies of human-caused mortality do not inform the larger body of cooperative breeding ecology and *vice versa*. Herein, we bridge these two areas of study with a synthesis about the effects of human-caused mortality on group characteristics, vital rates, and population states of cooperative breeders.

II. METHODS

We conducted a systematic review of the literature to identify relevant papers. We searched terms linking human-caused mortality and cooperative breeders using *Web of Science*, *Google Scholar*, *Primo*, and *World Cat* search engines. Additionally, we refined our search by using known cooperative-breeding species names and combinations of multiple terms and names that represent different parameters related to mortality and demography (Table 1). We had no restriction on years and used the literature cited within papers to assist us in finding other relevant works for our synthesis. We defined cooperative breeders, in line with common literature definitions, as: animals who live and breed in groups where non-breeding individuals help care for the breeders' offspring. Among vertebrates, cooperative breeding is expressed most prominently in birds and mammals. In this review, our focus was on cooperatively breeding terrestrial mammals, including carnivores, rodents, primates, suricates, pachyderms, and viverrids.

We retained publications with recorded vital rates or changes in demography due to human-caused mortality in cooperative-breeding mammals and categorized them to record effects on groups (e.g. family, pack) and populations (i.e. collection of groups) of the study species. For this synthesis, we did not include articles that only recorded behavioural responses to human-caused mortality or did not report an effect on a group characteristic (e.g. group size), vital rate (e.g. survival), or population state (e.g. lambda). We recorded the type of human-caused mortality for each species as general harvest (at random; e.g. big-game hunting season), poaching, population control (removing large numbers of a particular species from a population through aerial gunning or poisoning efforts with the goal of greatly reducing a population or extirpation), and selective harvest (the hunting of animals based on specific characteristics or physical traits). We considered mortality caused by vehicle collisions under general harvest due to the random nature of the mortality. We note that due to its cryptic nature, poaching is likely present in almost all the studies we summarize, but we only included papers in the poaching category if that source of mortality was the main focus of the paper. Finally, we excluded articles that used simulations to model the effects of human-caused changes to population demography.

III. RESULTS

We identified 58 published papers from which we could generate inferences for the effects of human-caused mortality on group characteristics, vital rates, or population states in cooperative breeders. Of papers reporting results on single species, 86% ($N = 50$) focused on cooperatively breeding carnivores. Canids comprised a majority of the single-species studies found (55%, $N = 32$) with African lions (*Panthera leo*; 21%, $N = 12$) and African elephants (14%, $N = 8$) the next most common (Table 2). We did not find relevant articles reporting vital rates or changes in demography due to human-caused mortality in studies focused on rodents, primates, suricates, pachyderms, or viverrid species.

Table 1. Search terms used to identify published literature on the effects of human-caused mortality on group characteristics, vital rates, and population states of cooperative breeders.

Term	plus	Term
Additive		Birth
Beaver		Birth rate
Blacked cap marmot		Bushmeat
Black mantled tamarin		Cooperative breeder
Breeder loss		Demography
Canid		Dispersal
Capybara		Emigration
Carnivore		Fecundity
Castor canadensis		Fidelity
Cooperative breeding		Foot-hold trap
Depredation		Harvest
Destabilization		Human-caused
Dhole		Hunting
Dingo		Immigration
Elephant		Inbreeding
Ethiopian dwarf mongoose		Infanticide
Felid		Maturity
Gambian mongoose		Mortality
Gold-and-white marmoset		Overharvesting
Golden jackal		Overhunting
Graells tamarin		Poaching
Group		Population
Group extinction		Recruitment
Group persistence		Reproduction
Helper loss		Survival
Highway mortality		Trapping
Human-caused mortality		
Human-wildlife interaction		
Hybridization		
Hyena		
Jackal		
Javan lutung		
Kin-based structure		
Kinship		
Lethal control		
Lion		
Livestock conflict		
Mating success		
North American least shrew		
Pack dynamics		
Predator control		
Predator management		
Protection		
Reproductive success		
Roadkill		
Rock-haunting ringtail possum		
Selective harvesting		
Social		
Social restoration		
Social structure		
Survival		
Thomas langur		
Trophy hunting		
Urban wildlife conflict		
White-headed marmoset		
Wied's marmoset		
Wildlife exploitation		
Wolf		

The most frequently reported types of human-caused mortality were general harvest (41%, $N = 24$) and poaching (41%, $N = 24$), followed by selective harvest (12%, $N = 7$) and population control (10%, $N = 6$; percentages total $> 100\%$ because four studies explicitly addressed more than one mortality source). Studies about general hunting typically focused on canids while selective harvest generally focused on African lions and poaching on African elephants. Control efforts typically targeted canids (Table 2).

Of studies reporting population growth or decline, 80% reported a link between human-caused mortality and population declines in cooperative breeders. Many of these studies did not identify the mechanism behind the population decline, but 28% of studies reporting population declines also identified concurrent declines in adult survival. Additionally, another 21% of studies reporting population declines documented concurrent declines in recruitment or reproduction. Nine studies reported that human-caused mortality led to an increase in breeder turnover (one listed no change), while six studies reported a decrease in group size and three reported a decrease in group persistence (Fig. 1, Table 2). Overall, changes resulting from human-caused mortality in populations of cooperative breeders were documented in a wide variety of ways with studies also reporting effects on population age structure, genetics, immigration rates, and sex ratios (Table 2). While there were generally not enough studies reporting the aforementioned vital rates to identify patterns, we do note that seven studies reported a change in age or social structure (including decreased genetic relatedness) and 15 other studies reported changes in immigration rates, genetic relatedness, or hybridization each of which are known potentially to affect social structure in group-living animals (Table 2).

General harvest yielded declining populations in six of eight reporting studies; one study reported no change, and two reported population increases ($N > 8$ because one study focused on both poaching and general harvest). Four of the seven studies that focused on selective harvest showed population declines and two of those reported decreased adult survival (Loveridge *et al*., 2007; Becker *et al*., 2013; Table 2).

Despite the stated goal of population control efforts (i.e. to reduce population size) only two out of six population control studies reported whether the treatment was effective (Woodroffe & Frank, 2005; Allen, 2015). Four population control studies did report declines in adult survival and three reported declines in reproduction, however (Table 2). Poaching is challenging to measure, but approximately 58% of studies in our synthesis showed a decrease in population size or growth rate due to poaching. Poaching also reduced litter size, recruitment, adult survival, and led to increased variation in pair bonding (Table 2). By contrast, two studies (on the grey wolf *Canis lupus* and African elephant) recorded population growth despite the presence of poaching (Wabakken *et al*., 2001; Dunham, 2008); both of these studies reflected a population recovering after recolonization (Wabakken *et al*., 2001) or after a severe reduction in population size (Dunham, 2008).

Table 2. Summary of the effects of human-caused mortality on group characteristics, vital rates, and population states of cooperative breeders. Sources of human-caused mortality were general harvest (random), poaching, population control (removing large numbers of a particular species from a population through aerial gunning or poisoning efforts with the goal of greatly reducing a population or extirpation), and selective harvest (the hunting of animals based on specific characteristics or physical traits).

Species	Source of human-caused mortality	Adult survival	Breeder turnover	Group persistence	Group size	Population change	Recruitment, reproduction, survival of young	Other	Reference
Canis lupus	General	—	Increased	—	—	—	—	Increased genetic diversity	Jędrzejewski *et al.* (2005)
Canis lupus	General	—	—	—	—	—	Decreased	—	Ausband *et al.* (2015)
Canis lupus	General	—	—	—	—	Increased	—	Increased immigration	Adams *et al.* (2008)
Canis lupus	General	—	—	—	—	—	Increased	—	Gude *et al.* (2012)
Canis lupus	General	—	No change	—	Decreased	—	Decreased	—	Ausband *et al.* (2017*b*)
Canis lupus	General	—	Increased	Decreased	—	—	Decreased	—	Borg *et al.* (2015)
Canis lupus	General	—	—	Decreased	—	—	Decreased	—	Cassidy *et al.* (2023)
Canis lupus	General	—	—	—	—	Decreased	—	—	Ballard *et al.* (1987)
Canis lupus	General	—	—	—	—	Decreased	—	—	Creel & Rotella (2010)
Canis lupus	General	—	—	—	Decreased	—	Decreased	—	Ausband *et al.* (2017*a*)
Canis lupus	Poaching	—	—	—	—	Decreased	—	—	Liberg *et al.* (2012)
Canis lupus	General	—	Increased	—	—	—	—	—	Milleret *et al.* (2017)
Canis lupus	Control	Decreased	Increased	—	—	—	Decreased	Decreased dispersal	Schmidt *et al.* (2017)
Canis lupus	Poaching	Decreased	—	—	—	—	—	—	Stenglein *et al.* (2018)
Canis lupus	General	—	—	—	—	—	—	Decreased genetic diversity	Rick *et al.* (2017)
Canis lupus	Poaching	—	—	—	—	Decreased in one area	—	—	Murray *et al.* (2010)
Canis lupus	General	—	—	—	—	—	—	Increased hybridization	Moura *et al.* (2014)
Canis lupus	Poaching/General	—	—	—	—	Decreased	—	—	Liberg *et al.* (2020)
Canis lupus	General	—	Increased	—	—	—	—	—	Žunna *et al.* (2023)
Canis lupus	Poaching	—	—	—	—	Decreased	—	—	Sunde *et al.* (2021)[a]
Canis lupus	Poaching	—	—	—	—	Increased	—	—	Wabakken *et al.* (2001)
Canis lupus dingo	Control	Decreased	—	—	—	Decreased	Decreased	Changed age structure	Allen (2015)
Canis lupus dingo	Control	—	—	—	—	—	—	Disrupted social structure	Wallach *et al.* (2009)
Canis lycaon	General	—	—	—	—	No change	—	Decreased kinship	Rutledge *et al.* (2010)
Canis lycaon	Control	—	—	—	—	—	—	Increased hybridization	Rutledge *et al.* (2012)
Canis mesomelas	General	—	—	—	—	—	—	Changed age structure	Minnie *et al.* (2016)
Canis mesomelas	General	—	—	—	—	—	—	Increased immigration	Minnie *et al.* (2018)
Canis mesomelas	General/Control	Decreased	—	—	—	—	—	—	Kamler *et al.* (2020)
Canis rufus	Poaching	Decreased	Increased	—	—	Decreased	Decreased	—	Sparkman *et al.* (2011)

(Continues on next page)

Table 2. *(Cont.)*

Species	Source of human-caused mortality	Adult survival	Breeder turnover	Group persistence	Group size	Population change	Recruitment, reproduction, survival of young	Other	Reference
Canis rufus	Poaching	—	Increased	—	—	—	—	Increased hybridization	Bohling & Waits (2015)
Canis rufus	Poaching	Decreased	—	—	—	Decreased	—	—	Hinton *et al.* (2017*b*)
Canis rufus	Poaching	—	Increased	—	—	Decreased	—	Increased hybridization	Hinton *et al.* (2017*a*)
Crocuta crocuta	Poaching	—	—	—	Decreased	—	Decreased	—	Benhaiem *et al.* (2023)
Loxodonta africana	Poaching	—	—	Decreased	—	Decreased	Decreased	Decreased genetic diversity	Archie & Chiyo (2012)
Loxodonta africana	Poaching	—	—	—	—	Decreased	Decreased	Changed age structure	Gobush *et al.* (2008)
Loxodonta africana	Poaching	Decreased	—	—	—	—	No change	Changed age structure	Wittemyer *et al.* (2013)
Loxodonta africana	Poaching	—	—	—	—	—	—	Decreased genetic relatedness	Wittemyer *et al.* (2009)
Loxodonta africana	Poaching	—	—	—	—	—	—	Decreased genetic diversity	Nyakaana *et al.* (2001)
Loxodonta africana	Poaching	—	—	—	—	—	—	Decreased genetic relatedness	Gobush *et al.* (2009)
Loxodonta africana	Poaching	—	—	—	—	Decreased	—	Skewed sex ratio	Wittemyer *et al.* (2014)
Loxodonta africana	Poaching	—	—	—	—	Increased	—	—	Dunham (2008)
Lycaon pictus	General	—	—	—	—	Increased	—	—	Woodroffe (2011)
Lycaon pictus	General	Decreased	—	—	Decreased	Decreased	Increased	—	Van Der Meer *et al.* (2013)
Lycaon pictus	General	Decreased	—	—	—	—	—	—	Woodroffe & Ginsberg (1999)
Lycaon pictus	General	Decreased	—	—	—	—	—	—	Woodroffe *et al.* (2007)
Lycaon pictus	General	—	—	—	—	Decreased	—	—	Woodroffe & Ginsberg (1998)
Panthera leo	Selective	Decreased	Increased	—	—	Decreased (males)	—	Increased immigration	Loveridge *et al.* (2007)
Panthera leo	Poaching/Selective	—	—	—	—	Decreased	—	—	Groom *et al.* (2014)
Panthera leo	Selective	Decreased	—	—	—	—	—	—	Becker *et al.* (2013)
Panthera leo	Selective/Poaching	—	—	—	—	—	—	Increased mortality risk	Loveridge *et al.* (2017)
Panthera leo	Selective	—	—	—	—	Decreased	—	—	Packer *et al.* (2011)
Panthera leo	Selective	—	—	—	—	Decreased	—	—	Croes *et al.* (2011)
Panthera leo	Selective	—	—	—	—	—	Increased	Skewed sex ratio	Mweetwa *et al.* (2018)
Panthera leo	Control	Decreased	—	—	—	Decreased	Decreased	—	Woodroffe & Frank (2005)
Panthera leo	General	—	—	—	—	Decreased	—	—	Van Vuuren *et al.* (2005)
Panthera leo	Poaching	—	—	—	—	Decreased	—	—	Green *et al.* (2018)
Panthera leo	Poaching	—	—	—	Decreased	Decreased	Decreased	—	Banda *et al.* (2023)
Panthera leo	Poaching	Decreased	—	—	Decreased	Decreased	—	—	Snyman *et al.* (2015)

[a] Study includes a relatively high rate of roadkill mortalities in addition to poaching.

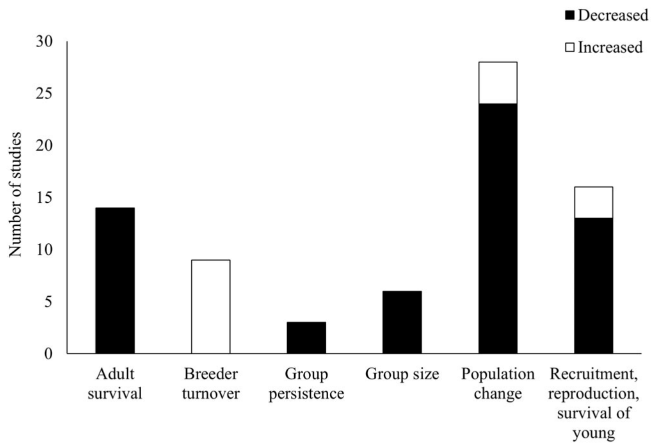

Fig. 1. Number of studies that reported increased or decreased group characteristics, vital rates, or population states associated with human-caused mortality in populations of cooperative breeders. Sources of human-caused mortality were general harvest (random), poaching, population control (removing large numbers of a particular species from a population through aerial gunning or poisoning efforts with the goal of greatly reducing a population or extirpation), and selective harvest (the hunting of animals based on specific characteristics or physical traits).

IV. DISCUSSION

One of the most apparent, and perhaps alarming, findings from our synthesis is that two subdisciplines in wildlife ecology, cooperative breeding and the effects of human-caused mortality, are separated. While our impetus for this synthesis was a desire to link these two seemingly isolated subdisciplines, we were still surprised to discover what little overlap exists between the cooperative breeding and human-caused mortality literatures. Because these two subdisciplines commonly work in isolation, our ability to accrue knowledge has been limited. For example, large numbers of grey wolves have been lethally removed from populations in Northwest Canada to promote survival of caribou (*Rangifer tarandus*; Hervieux *et al.*, 2014). Many such studies do not measure the response of lethal removal on the population of cooperative breeders themselves, only effects on their prey (Boertje *et al.*, 2017). We appear to be wasting opportunities to learn more about the environmental and evolutionary mechanisms driving group-living that could be leveraged through manipulative experiments of their populations. Similarly, using insights from cooperative breeding theory could help mitigate the effects of human-caused mortality on populations of cooperative breeders. For example, because of their disproportionate effect on population growth, the timing of human-caused mortality of breeders could be regulated in a population if it is found that they have increased mortality risk at certain times of year (Rebholz, Ausband & Waits, 2024). By embracing theory, managers could avoid the potential negative effects of breeder loss on group persistence and population growth.

Human-caused mortality was generally associated with declines in populations of cooperative breeders when studies reported such information. The strength of this effect likely depends on the rate of human-caused mortality, but this information was often not reported. Canid populations, in particular, appear to be able to grow at least under low rates of human-caused mortality (Woodroffe, 2011) while populations of *K*-selected species such as African elephants appear much more sensitive to human-caused mortality. Indeed, when reported, 6 of 13 (46.2%) studies of canids stated that human-caused mortality was compensatory at least to some degree. Poaching was commonly associated with negative effects in groups and populations of cooperative breeders. We note, however, that studies focused on the other aspects of human-caused mortality we considered (i.e. general harvest, selective harvest, and population control) almost certainly included some level of poaching as well. Thus, it appears that some, likely low, level of poaching may not markedly impact cooperative breeders. Indeed, grey wolf populations recolonized Scandinavia while human-caused mortality *via* poaching simultaneously increased (Wabakken *et al.*, 2001).

When population declines were reported, the underlying vital rate producing the change often was not. Different types of human-caused mortality may not be equal and the mortality of certain sex and age classes in a group could conceivably have disproportionate effects on populations of cooperative breeders (e.g. breeder loss; Brainerd *et al.*, 2008). Moreover, if management is to mitigate the potential negative effects of human-caused mortality in a population of cooperative breeders, it is critical to know which vital rate to influence through management (e.g. harvest timing or bag limit adjustments). Linking declines in populations of cooperative breeders to the underlying vital rate driving the decline would accelerate both learning and conservation.

There are many examples of kin selection as an influential factor facilitating group-living in mammals (Solomon & French, 1997). But there are also competing hypotheses such as mutualistic benefits of group size and group augmentation that may drive group-living (Kokko, Johnstone & Clutton-Brock, 2001). Even within a species or population, however, multiple forces driving group-living may arise at different times due to changes in the environment. For example, kin selection may predict aspects of group size and composition in a territorial carnivore at certain densities, but if human-caused mortality reduces density then group augmentation may become a better predictor of characteristics of group size and composition. Studies that manipulate populations of cooperative breeders could provide insights and further our knowledge about the basic ecology and evolution of group-living species. General harvest appears to be the most accessible way to address questions regarding how mortality might affect demography of cooperative breeders, but selective harvest or even population control events likely provide a better avenue for researchers to address the particular drivers and mechanisms that change certain vital rates.

Some of the most effective manipulative experiments in ecology have been removal experiments (i.e. removing individuals from a group and measuring the response) in cooperative breeders (Komdeur, 1994; Clutton-Brock *et al*., 2001). Given that we already have strong inferences from such studies, why should we spend time and resources on human-caused mortality as a *de facto* removal experiment? To date, removal experiments in cooperative breeders have been largely limited to birds and a few species of mammals. We do not yet know how transferrable such findings are to other species and ecological systems. By contrast, management actions occur in populations of cooperative breeders regularly around the world in different environments and ecological systems (Croes *et al*., 2011; Hervieux *et al*., 2014). Leveraging *de facto* removal experiments could conceivably yield different inferences across taxa and species but may also allow us to identify undiscovered patterns across a wider range of species and systems.

V. FUTURE RESEARCH

(1) Use insights from cooperative breeding theory to inform management actions for group-living species.

(2) Leverage management actions of cooperative breeders to expand existing cooperative breeding theory to include additional species and ecological systems. Such management actions occur regularly and exploiting these by establishing *a priori* hypotheses and, when possible, influencing the design of the management action, would be a cost-effective way to advance scientific discovery.

(3) We found a wide variety of group characteristics, vital rates, and population states measured in the studies included in our synthesis. Future efforts focused on the factors that influence group persistence would be useful because there are surprisingly few studies that measured the effect of human-caused mortality on this variable.

(4) Whenever feasible, it would be beneficial if management and research studies linked population declines in cooperative breeders to the underlying vital rate(s) causing the decline. Key group characteristics (i.e. size, composition, relatedness) could be measured whenever possible. Genetic and genomic sampling can often provide such data.

(5) We did not find relevant articles reporting vital rates or changes in demography due to human-caused mortality for rodents, primates, suricates, pachyderms, or viverrid species. Some species already provide opportunities to fill these gaps. For example, management actions removing or translocating beavers (*Castor canadensis*; rodent) are common where they come into conflict with human land use (Siemer *et al*., 2013).

VI. CONCLUSIONS

(1) Of the studies we reviewed, 80% reported a link between human-caused mortality and population declines in cooperative breeders.

(2) Studies often did not identify the mechanism behind population declines, but 28% identified concurrent declines in adult survival and another 21% reported concurrent declines in recruitment or reproduction.

(3) There was little overlap between the cooperative breeding and human-caused mortality literatures, limiting our ability to accrue knowledge.

VII. ACKNOWLEDGEMENTS

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