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ORIGINAL ARTICLE

Offspring sex ratios are male-biased reflecting sex-biased dispersal in Idaho, USA, wolves

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Abstract

Offspring sex ratios can vary widely across species, and the reasons for such variation have long intrigued ecologists. For group-living animals, predicting offspring sex ratios as a function of group and environmental characteristics can be challenging. Additionally, mortality of group members can upend traditional theory used to explain offspring sex ratios observed in populations. Gray wolves (*Canis lupus*) in Idaho, USA, are an excellent study species for asking questions about offspring sex ratios given their group-living behavior and persistent exposure to human-caused mortality. I hypothesized that offspring sex ratios would be influenced by the characteristics of individuals, groups, and populations. I generated genotypes for 419 adult and 400 pup wolves during 2008–2018. There was a significant male-bias in litters of wolf pups with nearly 12% more male pups born than females. The individual, group, and population variables I considered did not have significant associations with offspring sex ratios. Local resource competition helped explain offspring sex ratios in wolves in my study system, but not local resource enhancement theory. Although female helpers have been shown to help slightly more than males, offspring sex ratios did not favor the helping sex suggesting that the overall benefit of female helpers may have been negligible in wolf groups during my study. Three wolf groups consistently overproduced males, the dispersing sex, suggesting that habitat quality was poor in their territories. The male-biased offspring sex ratios observed throughout this population reflect sex-biased dispersal in wolves in Idaho. Such a pattern suggests breeding females may be reducing local resource competition (e.g., mates and successful reproduction) by producing more males than females.

Significance statement

Natural selection can favor biased offspring sex ratios in some species. This may be particularly true for animals that live and breed in groups such as gray wolves. Using genetic sampling, I show that offspring sex ratios in wolves are male-biased and reflect sex-biased dispersal in wolves. Breeding females may be reducing future local resource competition for mates by producing significantly more offspring of the dispersing sex (males).

Keywords *Canis lupus* · Gray wolf · Litter · Mating · Reproduction · Sex ratio · Wolf pup

Introduction

The ratio of males to females in a population can greatly affect population growth and demography (Mills 2013). Offspring sex ratios can vary widely across species, and the reasons for such variation have long intrigued ecologists (Fisher 1930; Hamilton 1967; Silk and Brown 2008). In many species, deviations from equal offspring sex ratios can be expected to return to 50:50 rather quickly as selection favors the rarer sex over the more common one (Fisher 1930). In group-living species where individuals within groups help provision and rear offspring, deviations from equal sex ratios may be the norm, however. For example, in groups with few members of the helping sex, breeding females may disproportionally produce more of the helping sex during reproduction, an example of local resource enhancement (Creel et al. 1998). Local resource enhancement predicts breeders will produce more of the sex that

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helps within groups. Philopatry and local resource competition can also skew offspring sex ratios because selection may act against overproducing the sex that stays near the parent and competes for resources (e.g., mates, food). Indeed, Silk and Brown (2008) showed that offspring sex ratios in primates favored the dispersing sex, an example of local resource competition where evolution favors the production of the sex that disperses.

Individuals can alter their offspring sex ratios and could conceivably do so as a function of their genetic composition. For example, a female with low genetic heterozygosity may produce more male offspring because her daughters will likely breed regardless, although Li et al. (2016) did not find this to be true in black-throated tits (*Aegithalos concinnus*). Additionally, when there is breeder turnover with a group, females may produce more male offspring to reduce the likelihood of future polygamy and having to share breeding in the group. In addition to the effects of individual decisions and behaviors, offspring sex ratios may vary with population density, an index for competition in a population. If population density is low and resources abundant, females may choose to produce more males if such males are more likely to mate given a larger size or improved body condition (Trivers and Willard 1973). Indeed, offspring sex ratios were male-biased in cooperatively breeding gray wolf (*Canis lupus*) populations at high densities compared to those at low densities (Mech 1975; Sidorovich et al. 2007).

For animals that live in groups, predicting offspring sex ratios as a function of group characteristics and environmental conditions can be challenging because relevant data are often lacking. Additionally, mortality of group members can upend traditional theory used to explain offspring sex ratios observed in populations. For example, local resource competition theory may predict producing fewer philopatric sex. If mortality disproportionately affects the philopatric sex, however, selection may work to favor offspring sex ratios where the philopatric sex is not underproduced. Human-caused mortality, in particular, can have large effects on the selective advantage of offspring sex ratios in wild populations (Holand et al. 2006). For many species, however, we often do not have offspring sex ratio data over long-time periods. This may be particularly true for carnivores that exist at low densities and are subject to frequent human-caused mortality making data collection difficult.

Gray wolves in Idaho, USA, are an excellent study species for asking questions about offspring sex ratios given their group-living behavior and persistent exposure to human-caused mortality in the form of hunting and trapping. I hypothesized that offspring sex ratios would be influenced by the characteristics of individuals, groups, and populations. Specifically, I predicted breeding female heterozygosity, and both male and female breeder turnovers would be associated with the production of more male offspring (Table 1). In contrast, I expected population density, harvest rate, litter size, number of helpers (i.e., nonbreeding adults) in the present year, number of adults (i.e., nonbreeding adults + breeding adults) in the previous year, pups recruited, sex ratio of helpers in the current year, and sex ratio of pups in the previous year would be associated with the production of fewer male offspring (Table 1).

Study area

I genetically sampled groups of wolves in three study areas (north, east, and south) in Idaho, USA, from 2008 to 2018 (Fig. 1). Annual temperatures ranged from − 13 to 36 °C (Western Regional Climate Center 2022), precipitation ranged from 30 to 130 cm (Western Regional Climate Center 2022), and elevation ranged from 646 to 3219 m. The northern study area (3189 km^2, Fig. 1) was comprised of forests of western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). The eastern (3388 km^2, Fig. 1) and southern (3861 km^2, Fig. 1) study areas were comprised largely of ponderosa pine (*Pinus ponderosa*), lodgepole pine, spruce mixed forests, and sagebrush (*Artemisia tridentata*) steppe. Wolves were harvested beginning in 2009 and annually each year thereafter with a brief cessation in 2010. Most wolves were harvested during September–March (Ausband 2016). Harvest averaged 18.4% over the study period and ranged from 10.4 to 27.6% of the population annually (Ausband 2021).

Methods

Field methods

Our behavioral inferences are made indirectly from genetic data collected in the field. It was not possible to record data blind because our study involved focal animals in the field. We collected wolf scats at wolf pup-rearing sites during summer (average sampling date, July 15). We located groups of wolves by surveying sites predicted by a pup-rearing habitat model (Ausband et al. 2010). When available, we used the Global Positioning System (GPS) or radio-telemetry locations of wolves that were radiocollared as part of population monitoring efforts by the U.S. Fish and Wildlife Service, Idaho Department of Fish and Game, and the Nez Perce Tribe. At potential pup-rearing sites, we first gave a series of howls (Harrington and Mech 1982) and then attempted to find an activity center (area where pups congregate) where fecal samples would be most abundant. Once an activity center was found we radiated out 500 m to sample additional scats (Jacobs and Ausband 2019). We attempted to resample each group every year from 2008 to

Table 1 Predicted associations between the sex ratios of litters of wolf pups (M to F) and hypothesized predictor variables

Variable	Predicted effect on the proportion of males in litter	Rationale
Breeding female heterozygosity (H_o)	-	Females with low diversity will have more males because female offspring will breed regardless of their diversity
Breeding male turnover between t-1 and t	+	Females in groups will have more males after breeding male turnover to reduce female competition for future breeding attempts when the breeding male position is refilled
Breeding female turnover between t-1 and t	+	Females in groups will have more males after breeding female turnover to reduce female competition for future breeding attempts
Density (wolves/1000 km^2), t-1	-	When population density is low and resources abundant, females may choose to produce more males if such males are more likely to mate given a larger size or improved body condition
Harvest rate, t-1	-	Females will produce fewer males as harvest rate increases because the number of helpers declines and selection will favor producing the helping sex (females)
Litter size, t	-	Females will produce fewer males in smaller litters because selection will favor producing the helping sex (females)
No. of helpers, t	-	Females will produce fewer males when the number of helpers is low because selection will favor producing the helping sex (females)
No. of adults, t-1	-	Females will produce fewer males when group size is small because selection will favor producing the helping sex (females)
Pups recruited between t-1 and t	-	Females will produce fewer males when fewer pups are recruited because selection will favor producing the helping sex (females)
Sex ratio (M to F) helpers, t	-	Females will produce fewer males when there is a male-biased sex ratio because selection will favor the less common sex (females)
Sex ratio (M to F) pups, t-1	-	Females will produce fewer males when there is a male-biased sex ratio in the prior year's litter because selection will favor the less common sex (females)

2018. We collected 125–200 samples per group per year, which generally detected every individual in the group (Stenglein et al. 2011). Sampling was conducted under the University of Montana IACUC (Animal Use Protocol 008-09MMMCWRU).

Laboratory methods

We performed DNA analyses at the University of Idaho's Laboratory for Ecological, Evolutionary and Conservation Genetics (Moscow, ID, USA). We initially screened all samples in a species-identification test using mitochondrial DNA to remove non-target species and low-quality samples. We then attempted to genotype all remaining samples using 18 nuclear DNA microsatellite loci (AHT103, AHT109, AHT121, AHT200, C05.377, C09.173, C37.172, Cxx.119, Cxx.250, FH2001, FH2004, FH2010, FH2054, FH2088, FH2137, FH2611, FH2670, FH3725: Holmes et al. 1994; Breen et al. 2001; Guyon et al. 2003; Salim et al. 2007; Ostrander et al. 2017). Further details regarding laboratory methods can be found in Stenglein et al. (2010a, b, 2011) and Stansbury et al. (2014). We analyzed all collected samples in 2008 and 2009. After 2010, we used rarefaction analyses (Stenglein et al. 2011) to subsample for economic efficiency and analyzed 40 adult and 25 pup samples from each group. If a group had more than two individuals detected only once, we analyzed additional samples when available to obtain 10 more consensus genotypes.

Analytical methods

In addition to estimating observed heterozygosity from the resulting genotypes using Program Genalex (Peakall and Smouse 2006) as well as group size, I determined maternity and paternity from pedigree analyses using Program COLONY, version 2.0.5.5 (Jones and Wang 2009). I included all sampled adult males and females as potential parents and all sampled pups as potential offspring for each year. I first calculated allele frequencies for a year in Program COANCESTRY version 1.0.1.5 (Wang 2011) and then imported those into Program COLONY for use in pedigree analyses. I allowed polygamy in both sexes and assumed an allelic dropout rate of 0.01. Tracking individuals over time provided information on breeder turnover, number of helpers, harvest rate, litter size, and population density in my study areas.

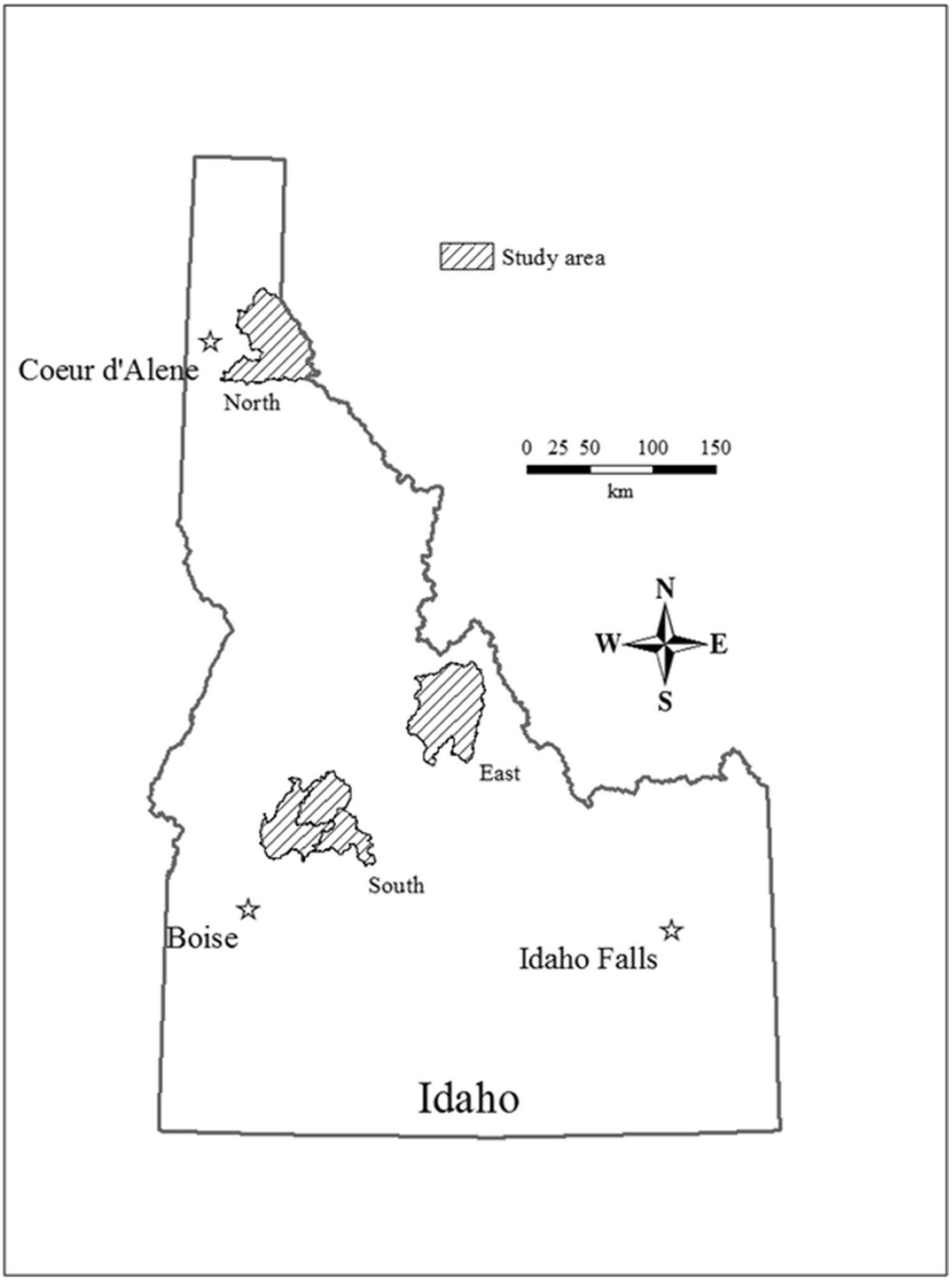

Fig. 1 Three study areas in Idaho, USA, where wolves were genetically sampled, 2008–2018

I used a chi-square test to first assess whether sex ratios of all wolf pup litters across all years were male-biased. I also tested for associations between the sex ratios of pups in each litter in each wolf group and several potential predictor variables (Table 1) using both generalized linear mixed effects and fixed effects models. I also tested for non-linear relationships by squaring (variable^2) several predictor variables in Table 1, namely, population density, harvest rate, number of helpers in a group, litter size, and number of adults in a group. I first standardized all variables using a Z-transformation for ease when comparing the resulting β coefficients. Finally, I compared competing models using Akaike's information criterion (AIC) and conducted analyses in Program R, version 4.0.4, with package "lme4"l (R Development Core Team 2021).

Results

I generated genotypes for 419 adult and 400 pup wolves across 80 wolf-group years. There was a significant male-bias in litters of wolf pups ($\chi^2=5.3$, df$=1$, $P=0.02$) with nearly 12% more male pups born than females during the 11 years (55.8%, $n=223$ vs. 44.3%, $n=177$, respectively; Fig. 2). There was just 1 year (2013) where females greatly exceeded male offspring numbers (proportions, 0.63 vs 0.38, respectively; Fig. 2), although I suspect this was due to sampling error ($n = 16$ pups total). Offspring sex ratios (M:F) did not appear to vary by study area (0.59, SD = 0.25; 0.55, SD = 0.17; and 0.53, SD = 0.26; east, north, and south, respectively; Fig. 1). Three wolf groups (Bumblebee, Hoodoo, Timberline II) with various breeders overproduced males consistently ($\bar{x} > 0.60$) and never had offspring sex ratios < 0.50.

Mixed effects models would not converge. A fixed effects global model with all variables (Table 2) except squared terms had the lowest AIC (87.97) and was nearly 10 AIC points lower than a model that included squared terms (AIC = 97.2). The top global model was nearly 25 AIC points lower than the null (AIC = 112.6). None of the individual, group, and population variables I considered had significant associations with the sex ratio of wolf pup litters (Table 2).

Table 2 Covariates value and significance from most supported model predicting the sex ratios of litters of wolf pups (M to F) in Idaho, USA, 2008–2018

Variable	β	SE	*P*
Breeding female heterozygosity (H_o)	0.14	0.35	0.70
Breeding male turnover between t-1 and t	−0.02	0.27	0.93
Breeding female turnover between t-1 and t	−0.05	0.33	0.87
Density (wolves/1000 km^2), t-1	0.11	0.38	0.77
Harvest rate, t-1	0.05	0.39	0.90
Litter size, t	0.06	0.33	0.86
No. of helpers, t	0.11	0.59	0.85
No. of adults, t-1	0.05	0.47	0.92
Pups recruited between t-1 and t	0.12	0.44	0.79
Sex ratio (M to F) helpers, t	0.04	0.48	0.94
Sex ratio (M to F) pups, t-1	−0.04	0.44	0.92

Discussion

Although not an a priori hypothesis, I found support that local resource competition could be used to help explain offspring sex ratios in wolves and I suspect that the local competition is primarily for mates. Male-biased offspring sex ratios reflect sex-biased dispersal in wolves and suggest breeding females may be reducing future local resource competition (e.g., for mates; Hamilton 1967) by producing more males than females without increasing overall litter size. Male wolves in my study population seldom inherit a breeding position within their group whereas females commonly do (Ausband 2022a, b). Male wolves generally disperse to find breeding opportunities and there is a strong male-bias in dispersal rates for wolves in my study area (Jimenez et al. 2017). Dispersal is not always male-biased in wolf populations, however (Morales-Gonzalez et al. 2021). Local resource competition theory predicts male-biased offspring sex ratios when dispersal is male-biased, which is precisely what I found. Breeding females also appear to monopolize breeding opportunities in groups of wolves as evidenced by increases in polygamy following breeding female turnover in my study system (Ausband et al. 2017). Selection via male-biased offspring sex ratios may therefore favor producing fewer philopatric females who compete for future mates and subsequent successful reproduction.

I found no evidence that local resource enhancement could be used to predict offspring sex ratios in wolves. Although female

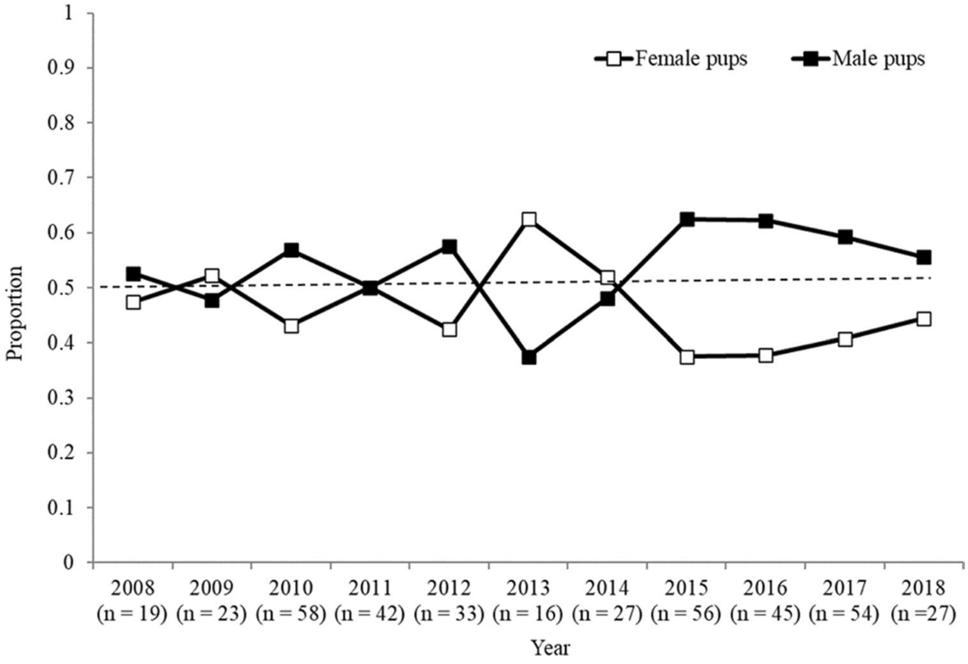

Fig. 2 Sex ratios of wolf pups ($n = 400$) in Idaho, USA, 2008–2018

helpers have been shown to help slightly more than males in wolf groups (Ausband et al. 2016), offspring sex ratios did not favor the helping sex (females) suggesting that the overall benefit of female helpers may have been negligible in wolf groups during the period of my study. This is not to say that some individual females within a group are not beneficial helpers, but there is little evidence that all females are beneficial helpers. In contrast, McNutt and Silk (2008) showed a strong male-biased sex ratio in groups of African wild dogs (*Lycaon pictus*) where males are known to help more and remain in groups longer than females. The sex ratio of harvested wolves is also strongly male-biased (55 M:45 F) early in the hunting season when most harvest is from rifle hunters (Ausband 2016). The ratio of wolves killed by rifle hunting nearly mirrors the male-biased estimates of offspring sex ratios. By the end of the harvest season, however, males were only slightly more commonly killed than females. In sum, it appears that breeding females are not overproducing the helping sex (i.e., females).

I considered a suite of individual, group, and population phenomena that could have potentially influenced offspring sex ratios but ultimately did not. If offspring sex ratios are largely driven by phenomena such as competition for mates or local habitat quality, then few of my explanatory variables would be expected to have predictive power with the exception of perhaps density (and group size and harvest indirectly). Although previous studies on canids found high density to predict male-biased offspring sex ratios and male-biased group composition (Mech 1975; Sidorovich et al. 2007; Iossa et al. 2009), I did not find an effect of density despite observing male-biased sex ratios in wolves. The overarching literature contains several hypotheses that might lead us to suspect skewed offspring sex ratios in cooperative breeders like wolves (Hamilton 1967; Creel et al. 1998; Silk and Brown 2008). Julliard (2000) showed that breeders may adjust offspring sex ratios as a function of local habitat quality. I did not measure habitat quality, but three wolf groups showed consistent patterns of overproducing males (e.g., Hoodoo wolf group, M to F ratio, $\bar{x} = 0.70$ and never < 0.50, 2009–2016). Following predictions of Julliard's model (2000), some wolf groups may have occupied poor quality territories and thus produced more of the dispersing sex. The Hoodoo group in particular vacated their territory and began to occupy a new territory beginning in 2016. Despite ongoing annual sampling to monitor them, they have not returned to their prior territory suggesting that it may have indeed declined in quality.

Many population and genetic projection models assume an equal sex ratio in wolves (vonHoldt et al. 2008; Miller 2017). Similar to other studies (Mech 1975; Sidorovich et al. 2007), I show that this assumption is not always valid and may depend on population density. Allowing for a male-biased sex ratio of offspring could greatly affect projection models given that male wolves appear to be the couriers of genetic diversity in wolf populations (Ausband 2022a). Additionally, a male-biased sex ratio could conceivably affect population projection models as fewer females would reach reproductive age.

We sampled wolves genetically using scats in summer, and some pups may have died prior to our sampling. Aside from starvation or abandonment in the den, pup mortality early in life is frequently related to disease outbreaks that can result in the entire loss of litters or nearly so (Mech et al. 2008; Almberg et al. 2010). I did not observe such disease outbreaks during my study and have no reason to suspect any form of early season mortality would affect one sex more than the other. Lastly, I note that we seldom found dead wolf pups during sampling at pup-rearing sites (< 1 pup per year over 11 years).

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Data availability Ausband DE (2022b) Wolf pup sex ratios and covariates, Idaho, USA, 2008–2018 [Data set]. Zenodo, https://doi.org/10.5281/zenodo.7035926

Declarations

Ethics approval Field sampling was conducted under the University of Montana IACUC (Animal Use Protocol 008-09MMMCWRU). All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Conflict of interest The author declares no competing interests.

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