Social relationships affect dispersal timing revealing a delayed infanticide in African lions

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Successful dispersal is a critical parameter for species persistence and evolution. Despite this, factors determining successful dispersal are poorly understood, particularly in wide-ranging species. Condition-dependent dispersal strategies tend to be more successful than fixed ones since they can entail dispersal occurring when an individual is most suited to doing so. However, the juvenile's family group or conspecifics may initiate premature dispersal, which could influence whether or not dispersal is successful. We studied dispersal in African lions and investigated 1) whether dispersal age affects dispersal success and 2) factors determining dispersal timing. We found that all males that dispersed before 31 months died during transience and that dispersal coincided, regardless of age or body condition, with the arrival of unfamiliar adult males. Whereas a high turn-over of territorial males is known to result in infanticide and eviction of sub-adults, our results indicate it can also induce a previously undescribed, 'delayed infanticide'.

Dispersal, the movement from a natal to a breeding site, is inherently risky and can entail a variety of direct or deferred costs (reviewed by Bonte et al. 2012). Despite this, some individuals do disperse, and those that survive to reproduce in a new social group influence a range of processes including population dynamics, gene flow and species distribution (Gillis and Krebs 2000). In light of increased habitat fragmentation and global warming, the importance of successful dispersal is increasingly apparent as it is often the primary mechanism by which metapopulations are sustained and new ones founded (Ronce 2007, Clobert et al. 2012). Successful dispersal is therefore a critical component for both species persistence and evolution. Despite its importance, the factors determining whether or not dispersal is successful are still poorly understood, particularly in large, wide ranging species.

Unsuccessful dispersal may occur due to the surrounding environment being unsuitable or too hostile, or when suitable habitats are too distant (Clobert et al. 2001). Dispersing individuals may increase the chance of successful dispersal by, for example, gathering information regarding the quality of their surroundings (Clobert et al. 2009), only dispersing if there is inter-patch connectivity (Bowler and Benton 2005), or through behavioural adaptations (Duckworth and Badyaev 2007). In addition, dispersing individuals may adopt condition-dependent strategies, triggered by individual phenotype (e.g. body size, fat

reserves), or environmental conditions (e.g. season, population density, habitat quality), or a combination of both (Ims and Hjermann 2001). Condition-dependent dispersal tends to be more successful than unconditional or fixed dispersal since plasticity in dispersal timing can entail dispersal occurring when an individual is most suited to doing so (Bowler and Benton 2005). For instance, European roe deer *Capreolus capreolus* and Belding's ground squirrels *Spermophilus beldingi* may only initiate dispersal once a critical mass has been attained (Holekamp 1984, 1986, Debeffe et al. 2012). It follows then that dispersing before attainment of a robust physical condition may incur increased costs (Stamps 2006). Indeed there is considerable literature on body size and its influence on dispersal which points towards a positive correlation between body size and dispersal ability (reviewed by Benard and McCauley 2008). In many species, body size is related to age and thus the age at which an individual disperses may also be a predictor of whether or not dispersal is successful (Waser et al. 1994).

If survival probability during dispersal increases with age, juveniles should delay dispersal (Tarwater and Brawn 2010). However, for this to occur their family group or conspecifics must allow them to remain or disperse voluntarily (Ekman 2006). Parent–offspring conflict and kin competition can force involuntary dispersal, with more intense competition when resources are limited or when population

density reaches a critical threshold. For instance, kin competition in combination with adult density has been shown to promote dispersal in common lizards *Lacerta vivipara* (Léna et al. 1998). If density-dependence is a limiting factor, it follows that juveniles from large litters are more likely to disperse (Harris and Trewhella 1988), and to disperse young (Hanby and Bygott 1987). In territorial species, the potential risks associated with early dispersal may be counterbalanced for bigger groups of dispersers, since larger groups usually overcome smaller groups, thus enhancing the likelihood of territory acquisition (Clutton-Brock 2002).

Parent–offspring conflict can entail parents initiating the dispersal of their offspring even under conditions where dispersal is risky, forcing dispersal at all costs (Johnson and Gaines 1990). In territorial species, such competition may be manifest with the arrival of unfamiliar adult males into the family group. For instance, in African lions *Panthera leo*, a male take-over of a pride results in the eviction or death of resident adult males and the infanticide of cubs (Packer and Pusey 1984, Loveridge et al. 2007). Incoming males will also kill or evict sub-adult males and those females that have not yet reached sexual maturity (Hanby and Bygott 1987, VanderWaal et al. 2009). Indeed, Hanby and Bygott (1987) found that the arrival of new males was highly correlated with dispersal initiation and it is likely that the unpredictable timing of pride take-overs resulted in the wide range of dispersal ages reported (20–65 months). However, the frequency at which pride take-overs occur could be exacerbated by anthropogenic perturbations such as conflict with pastoralists and trophy hunting. While high levels of anthropogenic mortality have been shown to result in increased infanticide (Swenson et al. 1997), it is plausible that it may also result in young, and therefore risky dispersal.

In this study, we investigated whether the turn-over of territorial male lions would have a knock on effect, a 'delayed infanticide', as sub-adults are forced to disperse regardless of age or condition, which may compromise their survival during dispersal. We examined the factors determining successful lion dispersal in Hwange National Park, Zimbabwe, an ecosystem where the lion population has been impacted by trophy hunting and is characterized by a high turn-over of territorial males (Loveridge et al. 2007, 2010, Davidson et al. 2011). The goals of this study were twofold: first, to assess whether the probability of surviving dispersal is a function of dispersal age, sex and/or group size; second, to investigate factors that may be related to the timing of lion dispersal, with a specific focus on the role of pride males and incoming males.

Methods

Study area and population

The study area (≈ 7000 km^2) was located in the northern section of Hwange National Park (HNP), Zimbabwe (19°00'S, 26°30'E). Vegetation consists primarily of woodland and bushland savannah (64%) and communities are dominated by *Baikiaea plurijuga*, *Colophospermum mopane*, *Combretum* spp., *Acacia* spp. and *Terminalia sericea*. The long-term mean annual rainfall is 613 mm (CV ≈ 26%) and generally falls between October and April. Surface water is available from seasonal waterholes, although only a few hold water year round. In the dry season water is artificially supplied to some (≈ 50) waterholes. We categorised three seasons consistent with previous studies in this area: early dry season (March–June), late dry season (July–October) and wet season (November–February).

Approximately 6000 km^2 of the study area is within HNP with the remainder in safari areas and agro-pastoral lands (Fig. 1). Trophy hunting occurs in the surrounding safari areas, with annual quotas reaching 60 lions between 1999 and 2004 (Loveridge et al. 2007). In 2005 lion trophy hunting was suspended to allow population recovery (Davidson et al. 2011). Trophy hunting resumed in 2009 with annual quotas of around 10 adult male lions. In addition, lions which kill livestock in the surrounding agro-pastoral lands are occasionally shot in management operations of Problem Animal Control. Alternatively they may be snared or poisoned by local agro-pastoralists (Loveridge et al. 2010). The source population has been monitored without interruption since 1999 and lion density is estimated around 3.5 lions per 100 km^2 (Loveridge unpubl.). The data used here were recorded from observations during the period 1999–2012 during which time 33 females and 43 males were fitted with GPS radio collars (see Loveridge et al. 2007 for details). Lion prides were regularly sighted and details of group composition and location recorded. Care was taken to individually identify lions during all sightings using whisker vibrissae spots and other distinguishing marks (Pennycuick and Rudnai 1970).

Dispersal data

Sub-adults were defined as individuals between 18 and 48 months old (consistent with Pusey and Packer 1987). The age of sub-adults was based on sightings of them soon after birth and is estimated to within one month. A total of 66 sub-adults (33 males and 33 females) in 28 different dispersal groups were observed to disperse from their natal pride. Dispersing lions were allocated a dispersal group identity (n = 28), and fifteen of these groups contained at least one collared individual. In two cases there was only one sub-adult in a pride, while in all other cases they dispersed together in groups (up to 13 individuals) that broke up, males and females splitting first, then into smaller groups. Dispersal group identity and dispersal group size were based on these subsequent splinter groups and not the original group that dispersed from the natal pride.

Age at dispersal was calculated as the mid-point between the last time a sub-adult was seen with its natal pride and the first time either was seen alone (mean time interval $\pm$ SD = 1 ± 1.5 months). A dispersing individual was deemed to have established a territory and therefore survived dispersal when it had been observed in an area for a minimum period of two months and reproduced thereafter.

Adult males

Consistent with Hanby and Bygott (1987) we considered two aspects of adult males as being important to the timing
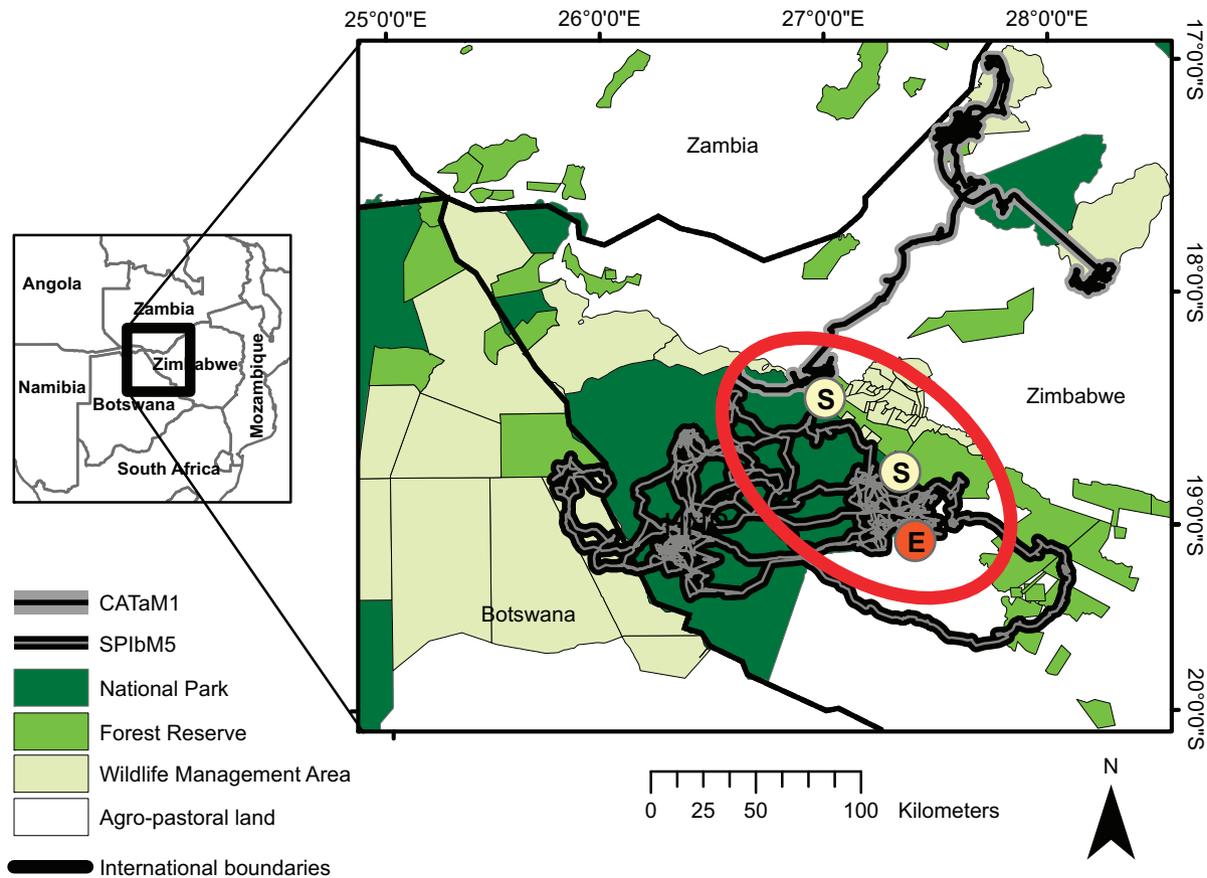
Figure 1. Map showing Hwange National Park (HNP) and surrounding forest reserves, wildlife management areas and agro-pastoral lands. The grey ellipse indicates the study area. Controlled lion hunting occurs in forest reserves and wildlife management areas (but not in Botswana). Lions that venture into agro-pastoral lands may sometimes be shot by management and frequently poached by communities. The trajectories detail the movement paths of two dispersing male lions (SPIbM5 and CATaM1 – both singletons). The letters in the circles denote start (S) and end (E) points for transience. CATaM1 was still dispersing at the time of writing this article.

of sub-adult emigration: the death or departure of the pride males and the arrival of unfamiliar adult males within the natal pride. We were interested in investigating whether the protection lost due to the absence of pride males resulted in sub-adult dispersal or whether this was more likely to occur once unfamiliar males made contact with the natal pride.

First we calculated the number of months between the death or departure of the pride male and the dispersal of sub-adults. Where coalitions of multiple pride males were present and died intermittently we used the timing of the last adult male to depart or be killed. In all dispersal groups where dispersal occurred in the absence of pride males the last remaining male of the coalition was collared and thus the accuracy of the date for their death or departure is estimated as (mean $\pm$ SD = 1 $\pm$ 0.9 month). We use the term 'pride male' to refer to territorial males which are presumed to be the fathers of all sub-adults within the pride, since they had been in attendance at the time of their birth.

Second we calculated the number of months between when an incoming male was first seen with adult females of the natal pride and the subsequent dispersal of sub-adults. We were able to accurately determine when unfamiliar adult males first came into contact with each natal pride

through the use of radio collars. In all but one instance at least one adult female from the natal pride was collared in addition to at least one adult male from the incoming coalition. In the case of one dispersal group, the incoming male was not collared but one of the adult females from the natal pride was. The use of radio collars enabled frequent sightings and the pairing of GPS data to establish first contact between the natal pride and incoming males.

Statistical analyses

Factors affecting survival during dispersal
We performed general linear models with a binomial error structure where our response variable was survived (1) or died (0). We created ten a priori candidate models to test whether survival during dispersal was a function of age at dispersal, sex of disperser, dispersal group size and combinations and interactions therein.

Determinants of dispersal age
We performed linear models with age at dispersal as the response variable. Our explanatory variables consisted of 1) a class variable for incoming male present or absent at the time of each dispersal event; 2) the number of sub-adults in

the natal pride at the time of each dispersal event; 3) sex of dispersers; 4) natal pride biomass – we used field data for adult weight (Loveridge et al. 2009) and growth equations for cub and sub-adult weight (Smuts et al. 1980); 5) the age of individual sub-adults when new cubs were born. We could not include a class variable for pride male present/absent at the time of each dispersal event as this variable was not independent of the variable incoming male present/absent: of the 66 recorded dispersal events, 21 occurred while the pride males were still in attendance and 45 occurred when the pride males had died or been evicted. Of these 45 events, 40 occurred after an incoming male had been sighted with the sub-adult's natal pride. In total we created 24 a priori candidate models including each of the main effects and combinations and interactions therein.

Relative roles of pride males or incoming males

To determine whether dispersal was triggered by the departure of pride male(s) or the arrival of new males we performed a paired t-test comparing the number of months between both scenarios and the commencement of dispersal.

For all models, dispersal group identity was used as a blocking factor. To identify the best model we used model selection based on Akaike information criterion corrected for small sample size (AICc). Where one model was clearly superior ($w_i > 0.9$) this was used, otherwise we obtained parameter estimates and unconditional confidence intervals by averaging across the models, correcting for model weights using R package AICcmodavg ver. 1.30 (Burnham and Anderson 2002, Mazerolle 2013). Finally, we performed separate chi-square tests to determine the distribution of dispersal timing across seasons. All statistical analyses were performed in R 2.15.1.

Results

Factors affecting survival during dispersal

Of the 66 recorded dispersal events, 49 individuals (28 males, 21 females in 21 dispersal groups), were recorded from emigration to settlement or death. The remaining 17 individuals (5 males, 12 females in seven dispersal groups) were observed to emigrate from their natal prides and disappeared. We therefore could not confirm whether or not they established a new territory and thus they were

not included in this analysis. Of the 49 individuals that were observed to settlement or death, 65% survived to establish a territory (17 males, 15 females) while 16% (n = 8) were poached and 10% (n = 5) were shot as 'problem animals'. One dispersing male lion died of natural causes (probably killed by an adult male) and three deaths were undetermined.

Whether or not dispersing sub-adults survived dispersal was best explained by an interaction between dispersal age and sex (Table 1). For males, successful completion of dispersal increased with the individual's age at dispersal (CI = 0.122–1.252; Fig. 2). The age at which sub-adult females dispersed had no effect on whether or not they survived to establishment, nor did the number of individuals in the dispersing group (estimate ± SE included 0 and 95% CI included 0; Table 1).

Determinants of dispersal age

The variables that were most influential in determining the timing of dispersal included the sex of sub-adult, presence of new males, and pride biomass (Supplementary material Appendix 1 Table A1). Overall there was a wide distribution of dispersal ages spanning over two years with sub-adult males dispersing when they were older (mean ± SD = 34.1 ± 7.4 months, range = 20–45, Fig. 3) compared to sub-adult females (mean ± SD = 30.2 ± 6.5 months, range = 18–45, Fig. 3; estimate ± SE = 3.001 ± 1.291; 95% CI = 0.471–5.532). Sub-adult males dispersed in smaller groups (mean ± SD = 2.6 ± 1.1, range = 1–6) compared to females (mean ± SD = 4.5 ± 2.6, range = 1–8) but neither group size, nor the birth of new cubs, had a bearing on the timing of dispersal.

Sub-adults dispersed earlier if incoming males were present (mean ± SD = 28.6 ± 6.1 months) compared to when no new male was present (mean ± SD = 37.6 ± 5.2 months; estimate ± SE = –4.554 ± 1.737; CI = –7.959– –1.150; Fig. 4). Pride biomass appeared in the top model, revealing a tendency for lower dispersal age with increased pride biomass (estimate ± SE = 0.003 ± 0.002; 95% CI = -0.835×10^{-5}–0.007). However the estimate ± SE included 0 as did the 95% CI; thus we considered sex and the arrival of immigrant males as the main factor influencing dispersal age.

A separate χ^2-test revealed that dispersal was markedly seasonal with more emigration occurring during the wet

Table 1. Summary statistics for models of survival to establishment during dispersal for African lions in Hwange National Park. Explanatory variables consisted of (1) 'disp.age' – age at dispersal; (2) sex of disperser; (3) 'G.S.' – number of individuals per dispersing group. Included are the log likelihoods, the AICc differences (Δi), the Akaike weights (wi) and the number of parameters (K).

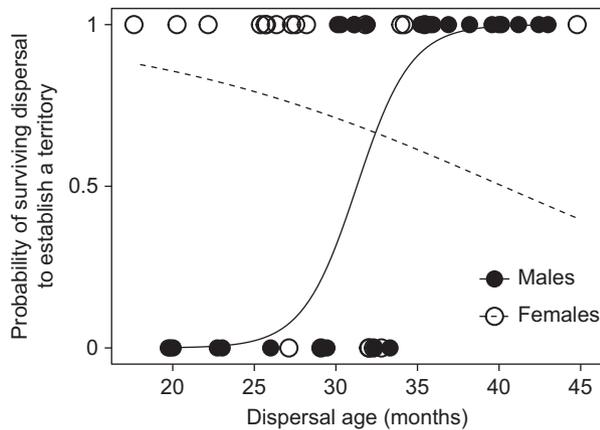| Response variable	Rank	Model	log likelihood	AICc	Δi	wi	K
Survived dispersal (1) vs died during dispersal (0)	1	disp.age × sex	−19.91	51.21	0	0.98	5
	2	disp.age + G.S.	−26.35	61.61	10.40	0.01	4
	3	disp.age	−28.11	62.76	11.54	0.00	3
	4	G.S.	−28.39	63.32	12.11	0.00	3
	5	disp.age + sex	−27.28	63.47	12.26	0.00	4
	6	disp.age + sex + G.S.	−26.27	63.93	12.72	0.00	5
	7	sex	−28.91	64.36	13.15	0.00	3
	8	Null	−31.63	65.35	14.14	0.00	1
	9	sex + G.S.	−28.39	65.70	14.48	0.00	4

Figure 2. Data (circles) and logistic regression curves (lines) showing the effect of dispersal age on the probability of surviving to establish a territory for both male and female sub-adult lions in Hwange National Park, Zimbabwe.

Figure 4. The age at which lions dispersed relative to the presence or absence of incoming males. Boxes show medians, 25% and 75% quartiles. Triangles indicate means. Whiskers indicate 10–90 percentiles. Dots represent the raw data.

season than in either the early dry or the late dry season ($\chi^2 = 7.363$, DF = 2, p = 0.025). Sub-adults of both sexes dispersed younger during the wet season (mean ± SD = 29 ± 5.8 months) compared to the early dry season (mean ± SD = 36 ± 4.6 months) or late dry season (mean ± SD = 34 ± 8.5 months).

Relative roles of pride males and incoming males

In the case of 34 dispersers, pride males were trophy hunted, and for 11 dispersers, pride males were evicted by incoming males (always when the coalition had been weakened either through trophy hunting or retaliatory killings). Sub-adult age at the time of pride male's death or eviction ranged from 1 to 37 months (mean ± SD = 15 ± 10.2 months). In order to determine whether new males encountering the pride or the death or emigration of the pride males was more likely to determine the timing of dispersal we analysed the subset of individuals which dispersed after

the pride male died and new males were seen with the natal pride (n = 40). The number of months between the death or eviction of resident males and new males being sighted with the natal pride ranged from 0 to 19 months (mean ± SD = 12 ± 8 months). A paired-samples *t*-test showed that there was a significant difference between the number of months to dispersal after the pride males had died or emigrated and after a new male was seen with the natal pride ($t_{1,39} = 8.97$; p < 0.001, Fig. 5). Once the pride males had died or been evicted the time to dispersal for the sub-adults was highly variable (mean ± SD = 14.6 ± 8.9 months, range: 2–40 months) while dispersal occurred far sooner after a new male was first seen with their natal pride (mean ± SD = 1.6 ± 3.2; range: 0-10 months). In fact, 63% (n = 25) dispersed within the same month that incoming males were first seen, and 26% (n = 9) dispersed a month later. Finally, a χ^2-test showed that the season during which dispersal most frequently occurred shifted from the late dry season when incoming males were absent to the wet
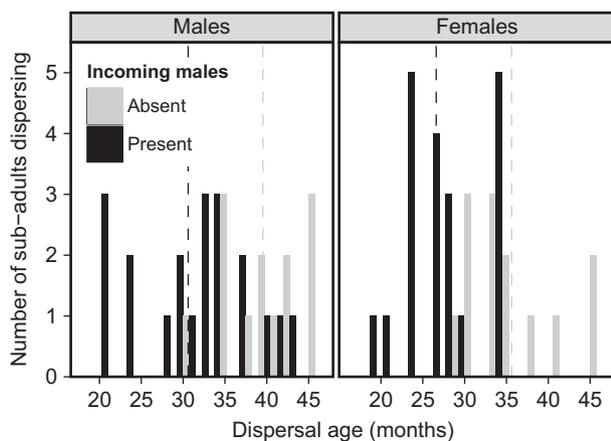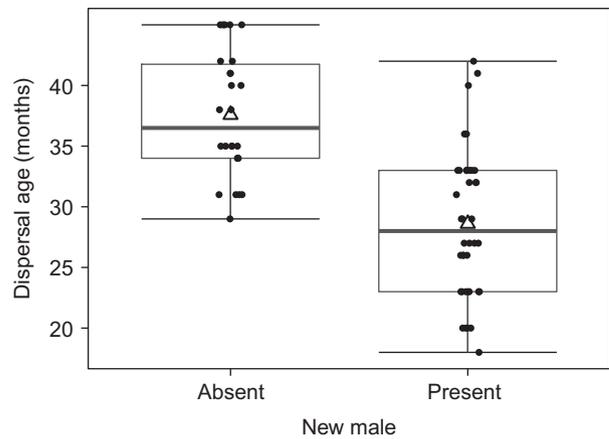

Figure 3. Dispersal ages for sub-adult lions in Hwange National Park, Zimbabwe. The data has been split to illustrate sex-specific dispersal ages depending on whether incoming males were present (black bars) and absent (grey bars) in addition to means (dashed lines) for each category.
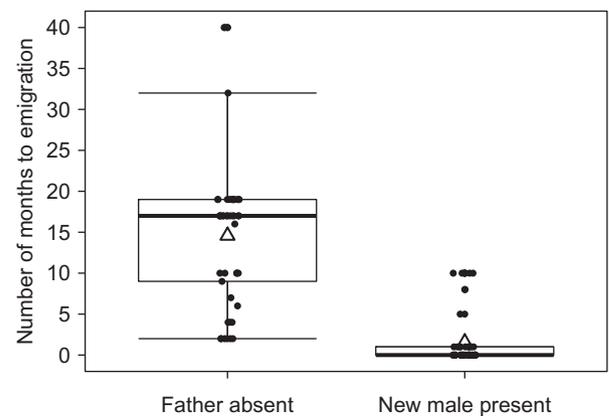

Figure 5. The number of months to emigration for sub-adult lions after the death/departure of the pride males and after a new male was first seen with their natal pride. Boxes show medians, 25% and 75% quartiles. Triangles indicate means. Whiskers indicate 10–90 percentiles. Dots represent the raw data.

season when incoming males were present ($\chi^2 = 17.271$, DF = 2, p < 0.001).

Discussion

Our results show that for sub-adult male lions the probability of successful dispersal increases with dispersal age as those that dispersed young generally did not survive. Males dispersed between 20 and 42 months of age, but all those that dispersed under 31 months of age died during dispersal. Interestingly, the regression curve linking survival probability with dispersal age was very steep indicating that dispersal delayed by even a few months can drastically increase survival probability (Fig. 2). For instance, a sub-adult male dispersing at 28.6 months (the average dispersal age when the pride male was absent) translates to a very low probability of survival (estimate $\pm$ SE = 0.17 $\pm$ 0.16). Just four months later survival probability increased markedly (estimate $\pm$ SE = 0.69 $\pm$ 0.14), and at the average dispersal age when the pride male was present (37.6 months), survival probability was very high (estimate $\pm$ SE = 0.98 $\pm$ 0.04). In contrast, the age at which female sub-adults dispersed had no bearing on whether or not they survived dispersal. However, for females the costs of dispersal may be delayed: for instance, Pusey and Packer (1987) found that female lions which dispersed were less likely to survive beyond eight years of age than those that were philopatric. That sub-adult males suffered high mortality if they dispersed when young is most likely due to their relatively small body size and inexperience. Lion body mass for males and females has a strong linear relationship with age ($r^2 = 0.98$ and 0.99 respectively) up until 36 months (Smuts et al. 1980). Thus male lions that disperse when they are relatively young are at a competitive disadvantage and are likely unable to compete for territory with older, larger males. This may prolong the amount of time and increase the distance travelled as vulnerable transients, which in itself could escalate mortality risk as reported for American martens *Martes americana* (Johnson et al. 2009). Since not all dispersing lions were collared, we could not accurately determine the date of establishment for all individuals and thus did not analyse the time length of dispersal. However, our data provide some support for this hypothesis: for instance, a lone male lion that dispersed at the age of 27 months was transient for 848 days and travelled some 4223 kilometres during the 16 months he was radio collared (Fig. 1). During his transience phase he spent considerable time outside the protected area and was subsequently shot for raiding livestock. A similar fate was recorded for 27% (n = 9) of our dispersing male study animals which were either shot as problem animals or subject to retaliatory killings. Thus our results are typical of a system impacted by trophy hunting and retaliatory killing, and hence characteristic of a population under anthropogenic pressure (Loveridge et al. 2010). In addition, increasing energy demands, coupled with hunting inefficiency, inexperience and inability to compete for occupied territories, may result in young dispersing lions taking more risks than older dispersers and adults. Indeed, studies in Namibia and Kenya have reported that dispersing sub-adult lions are more prone to stock-raiding than adults (Stander 1990, Patterson et al. 2003, 2004). Furthermore, studies that have reported mortalities during dispersal in other species frequently note that the cause is anthropogenic (Kenward et al. 1999, Real and Mañosa 2001, Klar et al. 2009, Smallwood et al. 2009).

Our findings are consistent with studies in other taxa that reported increased costs among young male dispersers (Waser et al. 1994, Ekman et al. 1999, Sparkman et al. 2011, Tarwater and Brawn 2010). For instance, Waser et al. (1994) reported that the survival rate of dispersing male dwarf mongooses *Helogale parvula* increased with age. While mongooses of both sex dispersed, only males had increased survival with dispersal age. Indeed, the costs of dispersal are expected to vary at an individual level according to sex (Bowler and Benton 2005). Our finding that female dispersal age had no bearing on their survival is typical of polygynous mammals, where females are less prone to mortality, particularly in sexually dimorphic species (Clutton-Brock and Iason 1986). That female lions dispersed younger than males was expected since sexually mature females are likely to remain and mate with immigrant males (Hanby and Bygott 1987).

Dispersal is a multicausal process, driven by individual characteristics and the environment, which likely act to alter the costs and benefits of dispersal (Matthysen 2012). In addition, the decision to disperse is often condition- or phenotype-dependent and may be triggered by an ontogenetic switch in physiology (Holekamp 1986). However, due to opposing forces acting on dispersal it is plausible that individuals in good condition may disperse early (Debeffe et al. 2012) or late (Hanski et al. 1991). In the present study it is clear that early dispersal was triggered by intraspecific competition, and lions were forced to disperse regardless of their age or size. It is possible that in the absence of incoming males other variables may have more influence. For instance, our study revealed a tendency for younger dispersal with increased pride biomass and VanderWaal et al. (2009) found that the probability of female lions dispersing increased with increasing pride size. In addition our study revealed that sub-adults dispersed when older in the dry season, which was also when dispersal most frequently occurred in the absence of incoming males. This leads us to tentatively propose that the dry season, a period of high resource availability, is an optimal dispersal time. Our results therefore suggest a scenario whereby, in the absence of incoming males, dispersal is likely to occur later and be more successful, with dispersal behaviour also possibly modulated by season and density-dependence, but that all condition- and density-dependencies are superseded by incoming males which force dispersal despite the costs. This concurs with a seminal experimental study on common lizards which showed that kin competition triggers dispersal irrespective of competitive ability and that the costs were reduced for larger individuals (Cote and Clobert 2010).

Similarly, the role of parental tolerance in delaying dispersal was experimentally shown in Siberian jays *Perisoreus infaustus* where the removal of fathers resulted in the dispersal of offspring, particularly when they were replaced by despotic immigrant males (Ekman and Griesser 2002). Our study takes such findings one step further to

show that age at dispersal has significant implications for survival, which may be particularly pronounced in ecosystems and species affected by a high off-take of adult males.

Free ranging populations that suffer high levels of anthropogenic mortality, such as our study population (Loveridge et al. 2010), experience an increased rate of male turnover, often resulting in infanticide (Swenson et al. 1997, Loveridge et al. 2007). Our study reveals a previously undescribed, indirect or 'delayed infanticide' that may be amplified in populations that experience a high off-take of resident adult males. In summary, it appears that the timing of lion dispersal is highly related to the presence of incoming males, leading to an increased mortality rate for male lions that disperse while young. It is plausible then, that in ecosystems with minimal off-take of adult males, dispersal would occur later and be more successful. These results have implications for the management of lions and should be considered in the same way as infanticide when setting hunting quotas for lions (Whitman et al. 2004).

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