Can survival analyses detect hunting pressure in a highly connected species? Lessons from straw-coloured fruit bats

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ABSTRACT

Animal behaviour, social structure and population dynamics affect community structure, interspecific interactions, and a species' resilience to harvesting. Building on new life history information for the straw-coloured fruit bat (*Eidolon helvum*) from multiple localities across Africa, we used survival analyses based on tooth-cementum annuli data to test alternative hypotheses relating to hunting pressure, demography and population connectivity. The estimated annual survival probability across Africa was high (≥ 0.64), but was greatest in colonies with the highest proportion of males. This difference in sex survival, along with age and sex capture biases and out-of-phase breeding across the species' distribution, leads us to hypothesize that *E. helvum* has a complex social structure. We found no evidence for additive mortality in heavily hunted populations, with most colonies having high survival with constant risk of mortality despite different hunting pressure. Given *E. helvum*'s slow life history strategy, similar survival patterns and rate among colonies suggest that local movement and regional migration may compensate for local excess hunting, but these were also not clearly detected. Our study suggests that spatio-temporal data are necessary to appropriately assess the population dynamics and conservation status of this and other species with similar traits.

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1. Introduction

"At Avakubi [Democratic Republic of the Congo], November 19, 1909, a flock of perhaps 100 had taken shelter for the day beneath the limb of a large tree, some 60 feet above the ground, where they were shaded by a mass of epiphytic ferns and orchids, and formed one great squirming mass. … After watching their amusing struggles for a while, we fired both barrels of a gun into their midst. We were standing almost directly beneath and for a few seconds it simply rained bats, dead or wounded. … Hundreds of them are then slain by the natives, who are fond of eating these bats".

Allen J A, Lang H, Chapin J (1917) The American Museum Congo expedition collection of bats (referring to *Eidolon helvum*, the straw-coloured fruit bat).

Demographic processes shape population dynamics and therefore have broad implications, for example on infection dynamics and sustainable harvesting capacity (Keeling and Rohani, 2008; Sandercock et al., 2011). Harvesting itself is hypothesized to shape demographic processes through various mechanisms (Sandercock et al., 2011). Under additive mortality, harvesting mortality has no effect on natural birth or death rates, and is additive to natural mortality in a linear fashion. Under compensatory mortality, density-dependent compensatory mechanisms (such as increased birth rates, decreased natural mortality, or increased movement) are evoked, meaning that harvesting adds no additional mortality to natural mortality rate. It is hypothesized that there should come a threshold at which these compensatory processes can no longer compensate and harvesting losses become additive (Sandercock et al., 2011). Understanding the contribution of compensatory or additive mortality processes is crucial for wildlife management and conservation so that offtake limits can be set to ensure harvesting does not deplete a population. Recent research has shown that fruit bats are a group of mammals that are hunted for food, sport or medicine in greater numbers than previously thought (Epstein et al., 2009; Harrison et al., 2011; Kamins et al., 2011; Mickleburgh et al., 2009). Correspondingly, studies on the sustainability of fruit bat bushmeat hunting are in their infancy compared with other terrestrial species.

Underlying demographic processes are often poorly elucidated in bats, even in common species. The straw-coloured fruit bat, *Eidolon helvum*, is one of the most common and widely distributed African bats, but is also widely hunted in parts of Africa (Anti et al., 2015;

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Carvalho et al., 2015; Kamins et al., 2011, Mickleburgh et al., 2009; Niamien et al., 2015). Demographic processes that affect whether hunting mortality may be additive or compensatory and their relevance for *E. helvum* fruit bats are considered under five different, but non-mutually exclusive, circumstances.

First, those species with slow life histories (long-lived with low fecundity, or so called 'K-selected' species), such as bats, primates, larger ungulates, and long-lived birds, are expected to suffer from additive mortality because they do not have the capacity to compensate for the additional mortality through reproductive surplus (Hamel et al., 2006, Sedinger et al., 2007, 2010). Hayman et al. (2012) estimated high annual adult survival rates and low fecundity for *E. helvum*, supporting expectations for a slow-life-history species.

Second, small or declining populations have limited compensatory capacity and are predicted to suffer from additive mortality (Bartmann et al., 1992). Significant *E. helvum* population declines have occurred in some areas of its sub-Saharan range, possibly because of habitat loss and over-harvesting for food and medicine (Mickleburgh et al., 2010, 2009; Perpetra and Kityo, 2009; Sodeinde and Soewu, 1999). Smaller, fragmented *E. helvum* populations also exist on a small number of offshore islands, including Pemba, off the Tanzanian coast (Hayman and Hill, 1971) and Príncipe, São Tomé and Annobón in the Gulf of Guinea (Juste and Ibanez, 1994). While Bioko Island in the Gulf of Guinea is close enough for bats to mix freely with the continental population, bats on Príncipe, São Tomé and Annobón islands are isolated and genetically distinct from one another (Peel et al., 2013). These smaller island populations may be more likely to suffer additive mortality in response to harvesting.

Third, migration and mixing among spatially structured populations can be a compensatory mechanism through demographic rescue (Cooley et al., 2009; Kvasnes et al., 2010). Continental *E. helvum* bats are seasonally migratory (Fahr et al., 2015; Funmilayo, 1979; Hayman et al., 2012; Mutere et al., 1980; Richter and Cumming, 2006; Thomas, 1983), and are capable of travelling >2500 km across international borders and up to 370 km in a single night (Richter and Cumming, 2008). In contrast, the isolated nature of the island populations (or other fragmented populations) might also make them prone to additive effects.

Fourth, harvesting during or immediately after periods of natural mortality is more likely to be additive than if conducted before such periods (Boyce et al., 1999; Kokko, 2001; Ratikainen et al., 2008). Hunting pressure is spatially heterogeneous across *E. helvum*'s range (Kamins et al., 2011; Mickleburgh et al., 2009; Peel et al., in press). *E. helvum*'s migratory behaviour includes a tendency to vacate and arrive in roosts *en masse* (Fahr et al., 2015; Hayman et al., 2012; Peel et al., in press; Richter and Cumming, 2006; Thomas, 1983), resulting in the shifting seasonal presence of an apparently abundant resource for hunters along these migration routes.

Last, individual susceptibility to harvesting may vary with the type and timing of harvesting; for example, specific hunting methods intentionally or unintentionally target specific age or sex groups (Boyce et al., 1999). A variety of hunting methods have been documented for *E. helvum*, including shooting, slingshotting, capture in nets and hitting individuals that have fallen to the ground (Kamins et al., 2011; Mickleburgh et al., 2009; Peel et al., in press), however, few comprehensive data exist on how roost structure varies with age and sex, and in different locations or different seasons.

Empirical investigations to directly estimate the effect of harvesting within a target species or population are complicated by these multifactorial responses. For example, comparison of population counts among populations with differing harvest rates has been used to detect whether harvesting is likely to be additive or compensatory (Bodmer et al., 1997). However, in the case of compensatory mortality, population counts alone cannot separate the contributions of potentially contributing density-dependent processes (e.g. altered birth rates, survival and movement). The necessity to disentangle the various processes that

contribute to population size when examining the effects of harvest on survival can be avoided by using mark-recapture techniques and harvest experiments (Bartmann et al., 1992; Cooley et al., 2009; Duriez et al., 2005; Obbard and Howe, 2008; Sandercock et al., 2011; Schaub and Lebreton, 2004; Servanty et al., 2010). These methods allow the effect of hunting to be anticipated by estimated harvesting rates and comparing those to survival rates under different harvesting pressures.

Logistical problems can preclude the possibility of using capture-recapture studies in some species, including bats. Instead, life table analyses enable population age structure, growth rate and survivorship patterns to be estimated and can allow for maturation of young and senescent mortality (Fieberg and DelGiudice, 2011; Kraus et al., 2013; Siler, 1979; Stolen and Barlow, 2003), thereby providing insight into the demographic processes of species for which cohort studies are not feasible. The flexible "Siler" model allows us to fit a function that includes maturation and senescence with a constant hazard (exponential) survival pattern as a base. The demographic processes relating to mortality for long-lived species, in which we might expect such maturation and senescence processes, can therefore be inferred in the absence of capture-recapture data.

Our expectations for long-lived species such as bats is that harvesting mortality will be additive. However, the highly connected colonies of *E. helvum*, determined through telemetry (Hayman et al., 2012) and inferred through population genetics (Peel et al., 2013), suggest that migration could be a compensatory mechanism that will overwhelm the local hunting pressure. In a companion paper, we provide new information on *E. helvum* colony sizes, hunting pressure, and age and sex structure for multiple colonies across tropical Africa (Peel et al., in Press). Here, we test hypotheses relating to hunting pressure and demography in this long-lived, yet highly mobile, species. First, we hypothesize that different host demographic structures and survival rates exist among regions and test whether this can be associated with different levels of local hunting pressure, or is likely related to other seasonal demographic and migratory processes. Second, we determine if mortality rates differ at different population sizes to make inferences regarding whether mortality through hunting is additive to natural mortality, or alternatively, that local movement and regional migration act as a compensatory mechanism. To test these hypotheses, we estimate harvest pressure and mortality risk across age classes from five different colonies across Africa and its outlying islands.

2. Methods

We used the background life history and hunting information for a subset of colonies of *E. helvum* across tropical Africa (Peel et al., 2016, and deposited in the online data repository, Dryad: doi:10.5061/dryad.2fp34). In particular, we present data from Accra (Ghana), Dar es Salaam (Tanzania), Morogoro (Tanzania), São Tomé (São Tomé and Príncipe), Príncipe (São Tomé and Príncipe), and Bioko (Equatorial Guinea) (Fig. 1). All fieldwork was undertaken under permits granted by national and local authorities (listed in the Acknowledgements section) and under ethics approval from the Zoological Society of London Ethics Committee (WLE/0489 and WLE/0467), using field protocols which followed ASM guidelines (Sikes et al., 2011).

Bats were either captured at the roost with mist nets as they departed the roost site at dusk (Ghana, Tanzania, Equatorial Guinea) or returned at dawn (Príncipe), or were shot by local hunters from roost or feeding sites (São Tomé). Morphometric (forearm length and weight) and demographic (age class, sex and reproductive status) data were recorded at the time of capture, and teeth were collected to determine age in years from tooth cementum annuli. Counting the cementum and dentine annuli was done by microscopy following histological preparation of tooth roots by Matson's laboratory, Milltown, Montana (Matson, 1993). Annuli were assumed to be deposited annually, based on other studies and the species strong seasonal migratory