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Demography of straw-colored fruit bats in Ghana

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Eidolon helvum is widely distributed across sub-Saharan Africa where it forms large, dense colonies. The species is migratory and satellite telemetry studies have demonstrated that individuals can migrate over 2,500 km. It is a common source of bush meat in West Africa and evidence of infection with potentially zoonotic viruses has been found in West African colonies. The species, therefore, is of interest to both ecologists and those interested in public health. Despite this, demographic parameters of the species are unknown. We focused our study primarily on a colony of up to 1,000,000 bats that roost in trees in Accra, Ghana to obtain estimates of birth rate and survival probability. Aging of bats by examination of tooth cementum annuli allowed use of life tables to indicate an annual survival probability for juveniles of 0.43 (95% confidence interval [*CI*] 0.16–0.77) and for adults of 0.83 (95% *CI* 0.73–0.93). Additionally, an annual adult survival probability of 0.63 (95% *CI* 0.27–0.88) was estimated by following 98 radiocollared bats over a year; capture–recapture data were analyzed using multistate models to address the confounding factor of emigration. True survival probabilities may be in between the 2 estimates, because permanent emigration may lead to underestimation in the capture–recapture study, and population decline may lead to overestimation in the life table analysis. Birth rates (0.96 young per female per year, 95% *CI* 0.92–0.98) and colony size changes were also estimated. Estimation of these key parameters will allow future analyses of both infection dynamics within, and harvest sustainability of, *E. helvum* populations.

Key words: capture–recapture, *Eidolon helvum*, multistate model, population dynamics, survival, tooth cementum

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Demographic parameters, such as survival and fecundity, determine dynamics of animal populations (Skalski et al. 2005; Stearns 1992). In long-lived animal species with low fecundity (K-selected species), population growth rate is most sensitive to adult survival and thus population persistence is typically highly dependent on adult mortality rates (Gaillard and Yoccoz 2003; Lande 1988; Lebreton and Clobert 1990; Saether and Bakke 2000). Harvesting and infectious disease epidemics may increase mortality rates above background levels. Also, demographic processes can determine if and how infections persist within populations (Keeling and Rohani 2008; Lloyd-Smith et al. 2005). It is therefore critical to have good estimates of host demographic parameters to understand infection dynamics (e.g., George et al. 2011; Keeling and Rohani, 2008) and likely impacts of harvesting (e.g., Kamins et al. 2011).

Estimating survival rates in wildlife is difficult. In part, this is due to the difficulty in aging wild animals, including bats, especially once the animals are sexually mature (Brunet-Rossini and Wilkinson 2009). Lack of knowledge regarding

animal ages prevents the use of life table approaches for survivorship analyses. Bats are particularly difficult to monitor, because of their cryptic characteristics and their frequent nonrandom temporary movements, such as seasonal migration. Individual marking (such as bands and tattoos) and morphological indices (such as tooth wear) have been used to identify and age bats (Kunz and Weise 2009). However, tooth wear is confounded by diet and is thus a poor indicator of age (Brunet-Rossini and Wilkinson 2009). Estimated maximum life-span data exist for only 65 of 1,100 known species of bat (O'Shea et al. 2004), all from individuals marked during their 1st year of life and fortuitously recaptured many years later. These data, however, are not robust quantitative estimates of survival probabilities (Brunet-Rossini and Wilkinson 2009).

O'Shea et al. (2004) cited 42 studies that included bat survival estimates, of which fewer than 10 used robust estimation techniques. Typically, these were based on capture–mark–recapture (CMR) surveys of open populations conducted over several years on species that display high roost fidelity and live in small, stable populations. These life-history traits enable relatively high recapture rates (Eberhardt 1969; O'Donnell 2009; O'Shea et al. 2004). More recently, several studies have attempted to fill this gap for some insectivorous bat species (Frick et al. 2007; Papadatou et al. 2009, 2011; Pryde et al. 2005; Schaub et al. 2007; Schorcht et al. 2009), but none has yet been conducted for fruit bats, which may have quite different life histories.

Eidolon helvum, the African straw-colored fruit bat, is an Old World fruit bat of the family Pteropodidae (Giannini and Simmons 2003) and is distributed throughout sub-Saharan Africa (DeFrees and Wilson 1988). Tropical forests are presumed to represent its primary habitat; however, it migrates annually, perhaps to savannah regions along a north–south axis (Richter and Cumming 2006, 2008; Thomas 1983). It is thought that food availability may be the driver of this migratory pattern (Richter and Cumming 2006). *Eidolon helvum* frequently roosts in enormous colonies: a colony in Kasanka National Park, Zambia, is estimated to reach between 5 and 10 million bats (Sorensen and Halberg 2001). The species is harvested for bush meat, particularly in West Africa (Funmilayo 1978; Kamins et al. 2011; Mickleburgh et al. 2009). We recently estimated that at least 128,000 *E. helvum* are harvested annually in southern Ghana alone, and it is unknown if current harvest rates are sustainable (Kamins et al. 2011). In addition, *E. helvum* is of interest to those working in fields of public health and emerging infectious diseases. Serological evidence of infection with potentially zoonotic viruses, including Lagos bat virus (a rabies-related lyssavirus), henipaviruses, and Ebola virus, has been found within a single colony of *E. helvum* in Accra, Ghana (Hayman et al. 2008a, 2008b, 2010).

The aim of this study was to estimate demographic parameters, specifically survival and birth rates, in the *E. helvum* population in Accra, Ghana. We chose this population because of its proximity to humans, its known use as a source of bush meat, and serological evidence of circulating viruses within the colony. We hypothesized that the species is K-selected (Barclay and Harder 2003; O'Donnell 2009) with low fecundity and high survival rates, and is thus highly susceptible to overharvesting. Colony size was monitored during the study period because of its importance for both conservation assessment and infection persistence.

Materials and Methods

Ethical approval for this project (WLE/0467) was received from the Zoological Society of London Ethics Committee and locally from the Wildlife Division of the Forestry Commission, Ghana, and followed ASM guidelines (Sikes et al. 2011).

Data collection location and dates.—All data were collected in the Republic of Ghana, West Africa. Data for colony size estimates were collected from January 2008 through January 2010; other demographic data were obtained from January 2007 through July 2010. The main study site was a large *E. helvum* roost in central Accra (05°35′N, 00°11′W), with additional roosts studied in Kumasi (06°41′N, 01°37′W) and Tanoboase (Tano Sacred Grove; 07°39′N, 01°52′W). These colonies are at their maximum size during the dry season (typically November to early April in southern Ghana). Kumasi is approximately 200 km from Accra and the colony comprised around 500,000 bats, roughly half the size of the Accra colony when first visited in 2007. The Tanoboase colony was unknown before this study; it is located ~300 km from Accra and 100 km from Kumasi. The degree of colony connectivity was unknown before this study. *Eidolon helvum* is a seasonal breeder with copulation previously reported to occur from April to June (Mutere 1968), followed by parturition from February to May the next year. Data were collected from late January to early February, and from late March to early April, corresponding to early and late pregnancy periods, respectively, in Ghana (D.T.S. Hayman, pers. obs.). Further data collected in July and November correspond to periods when the majority of the colony had migrated and then returned from migration, respectively.

Colony size estimates.—Colony size was estimated by visual counting during the day when bats were roosting in trees in Accra. Counts started after 0900 h and finished before 1630 h because bat activity within the colony was lowest during these hours and therefore movement did not lead to obvious double counting or the missing of large numbers of individuals. Counts were performed on an ad hoc basis when bats were being sampled for virological purposes by a single author (DTSH), but estimation of the numbers of bats in a sample of trees by 3 other researchers during the study period gave colony sizes in the same order of magnitude.

Because of the large number of bats roosting in dense aggregations, it was impossible to count all individuals accurately. Colony size estimates were therefore made by scaling up counts from individuals through clusters and branches to whole trees. Bat clusters in Accra (Fig. 1) typically comprised 8–100 bats, as reported previously (DeFrees and Wilson 1988). The product of this and the number of occupied

Fig. 1.—Cluster of roosting *Eidolon helvum* in the city of Accra, Ghana.

branches per tree was then used to estimate number of bats per tree, and finally the product of this and the number of occupied trees was used to estimate the total number of bats (Vardon and Tidemann 2000). This was performed for each tree in the colony on the day of the count because the number of trees occupied by bats fluctuated and the trees the bats chose to roost in changed throughout the study. Also in 2008 we estimated the size of the colony at Tanoboase, another very large colony, by counting the number of trees with bats in and using the average number of bats per tree in Accra, on the basis of our observation that tree size and roosting density appeared similar in both places. This colony was assessed because of its large size and because it was previously not cited in any literature.

Capture and sampling method.—Bats were caught by erecting mist nets between treetops. Nets were erected during the day and bats were caught between 0300 h and 0700 h when they returned to the roost from foraging. Bats were captured as part of an ongoing study between 2007 and March 2010, during which 1,306 individuals were caught. Each trapping session was performed over 3 nights, and approximately 100 individuals were caught and sampled during each session. Sampling sessions were performed in January/February 2007–2010, March/April 2008–2010, July 2009–2010, and November 2008–2009. Each bat was carefully removed from the net after capture, placed in a separate pillowcase, weighed, and hung off the ground, under shelter, before processing. Sex, breeding status, and age category were determined by direct observation, and each bat was individually marked using either a thumb band or a ball–chain necklace (Porzana Limited, Icklesham, United Kingdom) before release (Kunz and Weise 2009; Tidemann 1999; Vardon and Tidemann 2000). Morphological features allowed categorization into neonate, juvenile, and sexually immature (SI) or sexually mature (SM) adult groups (DeFrees and Wilson 1988). Sexual maturity of adult bats was determined on the basis of testicular or mammary development.

Eighty-eight bats were euthanized under general anesthesia between January and July in 2008 and 2009 for studies of potentially fatal zoonotic viruses that required postmortem organ tissues for analysis. This provided an opportunity to obtain teeth for aging the bats using analysis of cementum annuli (Divljan et al. 2006), as explained below. A voucher specimen is held in storage at the Ghanaian Veterinary Services Directorate, Accra, Ghana. Teeth were frozen at –70°C before transport, and dried before processing (Matson's laboratory, Milltown, Montana).

Birth rates.—Reproductive biology of *E. helvum* has been studied extensively in Nigeria where only 1 offspring is born per female per year (Funmilayo 1979; Mutere 1965, 1967). Assessing proportion of females breeding each year provides a proxy for birth rate. When female bats were caught, pregnancy was determined by abdominal palpation. Just before migration (late March and early April) the majority (52/53) of pregnant females caught in Accra were near term, and we did not catch any females with suckling neonates. Thus we estimated pregnancy rates by combining data collected from late January to early February with those collected from late March to early April, which corresponded to early and late pregnancy periods, respectively. This allowed us to estimate pregnancy rates from 182 females (Table 1). Assuming that all detected pregnancies resulted in a live birth, we deduced the birth rate from the colony size and the proportion of females

Table 1.—Number of pregnant bats detected by abdominal palpation in female *Eidolon. helvum* (data from 2008 and 2009 are combined).

Pregnant	January	February	March[b]	Total
Total sampled	88	41	53	182
Proportion pregnancy detected	0.95[a]	0.93	0.98	0.96

[a] Three possible positive findings were included as pregnant for this analysis.

[b] A single bat was sampled in April but during the same sampling event.

pregnant at time of capture. The postmortem analysis of 88 bats included 14 pregnant females.

Age determination by tooth cementum annuli.—Counting annuli in cementum and dentine has been used to age *Pteropus alecto* and *P. poliocephalus* (Brunet-Rossini and Wilkinson 2009; Cool et al. 1994; Divljan et al. 2006). These studies also found that canine teeth produced better results than other teeth. Canine teeth from 88 euthanized bats were aged by histological cementum annuli analysis (Matson's laboratory, Milltown, Montana; Fig. 2), assuming that annuli were deposited annually (Cool et al. 1994). Six of 88 individuals were not from Accra, but from Kumasi ($n = 3$) and Tanoboase ($n = 3$), and were included in the study once radiotelemetry data (see below) demonstrated that animals moved among these 3 colonies.

Adult survival.—To estimate annual adult survival probability from age frequencies, and to test whether there was evidence for variation in survival probability with age after the 1st year, we fitted life table models to age frequency data derived from tooth cementum annuli data, assuming a stationary age structure. We tested 4 candidate models based on competing risks models proposed by Siler (1979). This approach assumes a constant baseline mortality risk operating throughout life and considers 2 additional factors: a decreasing risk in early life (maturation), and an increasing risk in later life (senescence). Annual probability of survival at age x under constant baseline risk is given by:

$$l_{x,2} = \exp(-a_2 x)$$

and maturation and senescence elements are defined respectively by:

$$l_{x,1} = \exp([-a_1/b_1][1 - \exp\{-b_1 x\}])$$

$$l_{x,3} = \exp([-a_3/b_3][1 - \exp\{b_3 x\}])$$

where a is the initial hazard for each element, b is the rate at which hazard decreases or increases with age during maturation or senescence, respectively, and x denotes age in years. Subscripts 1–3 denote respectively maturing, constant, and senescing elements. Overall survivorship is then given by the product of desired components, such that the 4 models tested were constant risk ($l_x = l_{x,2}$), maturing risk ($l_x = l_{x,1}\ l_{x,2}$), senescing risk ($l_x = l_{x,2}\ l_{x,3}$), and both maturing and senescing risks ($l_x = l_{x,1}\ l_{x,2}\ l_{x,3}$).

Assuming a stationary age structure and population size, the expected proportion P_x of the population in a given age group x is proportional to that age group's survivorship relative to the sum across all ages (y). More generally, population size varies annually by a constant factor λ, and the expected age structure converges toward a stationary distribution given by:

$$P_x = \frac{l_x}{\lambda^x \sum_{y=0}^{\infty} l_y/\lambda^y}$$

(Caughley 1977). Given observed numbers of animals in each age class, f_x, derived from tooth cementum annuli, the log-likelihood for a given survivorship function P_x follows a multinomial distribution:

$$L = \frac{(\sum f_x)!}{\Pi f_x!} \Pi P_x^{f_x}$$

Each model is fitted to data by maximizing the log-likelihood function with respect to the parameters of the underlying survivorship function. It is not possible to estimate survivorship parameters and population growth rate simultaneously using this approach (Caughley 1977). Therefore, we fixed λ to allow estimation of survivorship, although we have no information on population trend. We therefore explore effects

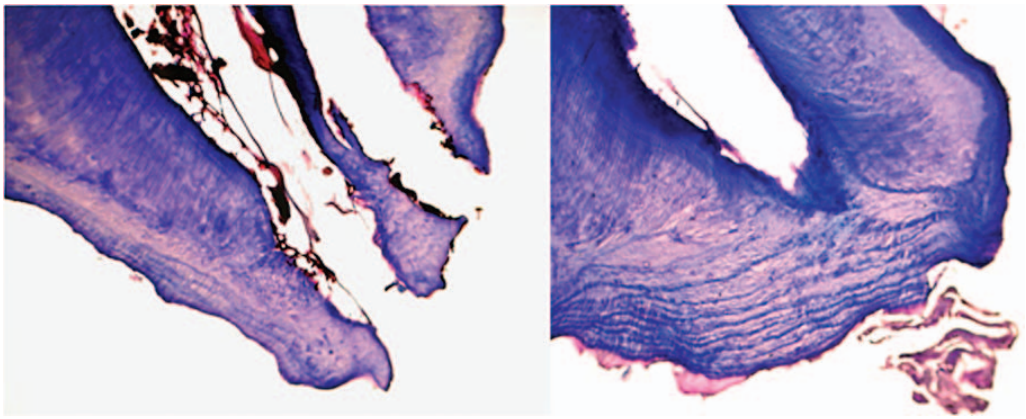

Fig. 2.—Cementum age analysis of Ghanaian *Eidolon helvum*, showing a bat with 2 (left) and 9 (right) cementum annuli at the root tip. Tooth preparations and figure prepared by Matson's Laboratory, Milltown, Montana.

of varying λ on survival rate estimates, bracketing decreasing, stable, and increasing population assumptions. Using an information theoretic approach, support for alternative models with survival rates either constant or changing with age is assessed by the Akaike information criterion (AIC; Burnham and Anderson 1998).

Juvenile survival.—Because no juveniles were recaptured during the period of study and none were therefore part of the CMR telemetry study, juvenile survival was estimated using a single sex (female), postbreeding, density-independent Leslie matrix (Caswell 2001), assuming constant adult survival, and assuming that animals give birth when they reach 2 years of age (i.e., there are 3 categories, juvenile [(N_0], sexually immature [N_1], and sexually mature [N_2]):

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \end{bmatrix} = \begin{bmatrix} 0 & sp & sp \\ s_0 & 0 & 0 \\ 0 & s & s \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \end{bmatrix}$$

where $N_{x,t}$ = population size in age class x at time t, s_0 = juvenile survival rate, s = adult (ages 1 and older) survival rate, p = birth rate, assuming all mid- to late-term pregnancies result in live birth of 1 neonate.

We then fixed adult survival and birth rate parameters to estimates derived from tooth cementum annuli and CMR (see below) data and estimated birth rates from this study, and constrained the dominant eigenvalue (N_{t+1}/N_t) $\lambda = 1$. This allowed us to numerically estimate for s_0 using $s_0 = (1 - s)/sp$.

Radiotelemetry and CMR modeling.—Life table analyses are prone to bias if the assumption that the population has a stable age distribution is violated. This is why CMR studies are strongly recommended for estimating survival (Williams et al. 2002). Because of low recapture rates in very large populations (e.g., Towner et al. 2009), we used radiotelemetry to mark and locate animals. We fitted a total of 98 radiotransmitters to adult bats, using collars weighing approximately 9 g in total (less than 4% body weight) and emitting within a 150/151 MHz range (Wildlife Materials Inc., Murphysboro, Illinois). The receiver was a 138–174-MHz SIKA receiver (Biotrack Ltd., Wareham, United Kingdom). Sixty-three transmitters were fitted in January 2008 (15 SM and 7 SI females, 36 SM and 5 SI males) and a further 35 in March 2008 (10 SM and 2 SI females, 18 SM and 5 SI males). Each transmitter had a >420-day battery life, which allowed us to detect bats as they returned to the Accra colony after the migratory period, and therefore estimate annual apparent survival probabilities.

Location of tagged bats was carried out both day and night to ensure that individuals detected during the day were leaving to feed at night (assumed to be alive), although this approach does not distinguish between tag loss and death within the colony. Initial intensive daily searching throughout the colony in Accra determined that some bats did not return to the colony each day. Recapture data were collected approximately weekly in the Accra colony from January 2008 to July 2009 (maximum 73 weeks). For survival analysis, however, these 73 weekly data were combined to provide monthly recapture probabilities: individuals were classified as alive if they were detected at any time in a given month. Only the first 12 months of data were used because of low sample size after migration in March 2009. Other known *E. helvum* colonies in Ashanti, Eastern, Brong-Ahafo, and Volta regions were visited in January and April 2008 and in January, March, and April 2009 and checked for presence of radiotagged bats. In particular, 6 searches were performed in the Kumasi colony and 4 in Tanoboase.

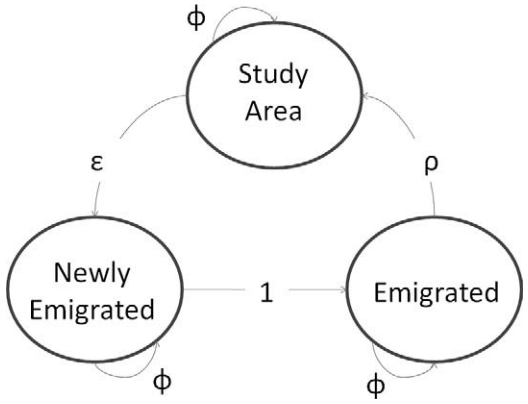

FIG. 3.—Transitions for the multistate model, with survival (φ), emigration (ε), and return (ρ) parameters shown. The gray circles represent unobserved states within which individuals cannot be encountered. Once emigrated, individuals move from "newly emigrated" to "emigrated" with a probability of 1.

We initially fitted a Cormack–Jolly–Seber (CJS) model using the package U-CARE (Choquet et al. 2009), allowing estimation of apparent survival in open populations; however, quality of fit was poor (Appendices I and II). The model suggested that those individuals released in the March cohort during the period of migration (March 2008) had significantly different recapture probabilities than those released in January 2008. This recapture heterogeneity is most probably due to individuals leaving the study area for a period of time, before returning later. Because of the overall significant lack of fit of the CJS model we then used a multistate Arnason–Schwarz model (Arnason 1973; Schwarz et al. 1993) to estimate the emigration probability of individuals, presumed to be the key underlying source of heterogeneity in capture probability. This model allowed us to estimate monthly survival probability (φ), which could then be transformed to annual survival (using φ^{12}) if constant (see Results). Model selection was performed using AIC.

For the multistate modelling, we defined 3 states (Fig. 3): study area—in this state individuals are available for capture; newly emigrated—if individuals leave the study area, they first enter this state. This state is unobservable and recapture probabilities were constrained to zero; and emigrated—after individuals have moved to the newly emigrated state, they progress to this state. This state is also unobservable.

Rationale for incorporating 2 emigrated states was to constrain individuals to emigrate for at least 2 consecutive time periods, to differentiate between animals that remain

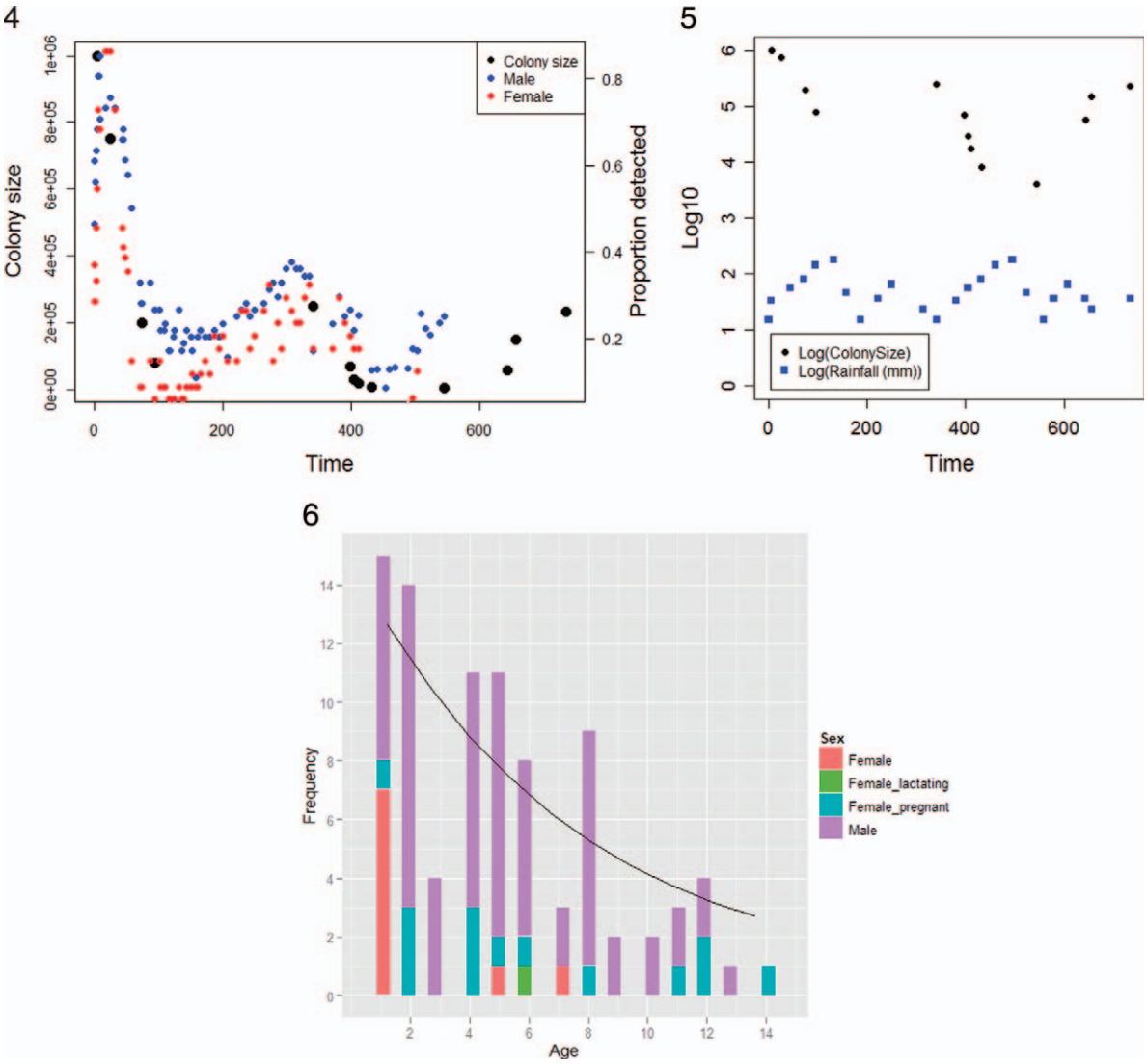

Fig. 4–6.—Colony size estimates and proportions of male and female radiotagged *Eidolon helvum* detected in Accra, Ghana. Time is shown in days. Fig. 5. Log(colony size estimates) with log(rainfall in millimeters) is shown to demonstrate the seasonal patterns of both in Accra, Ghana. Time is shown in days. Fig. 6. Age distributions of *Eidolon helvum* determined by canine tooth cementum annuli analysis. The overlaid curve is the fitted exponential survival function with a constant survival rate of 0.83. The ages of 15 breeding females, sampled during the breeding season, are given.

within the study area but are not recaptured, and those that truly emigrate. We therefore constrained the model by selecting a fixed time interval during which a proportion of individuals emigrate; the latest possible emigration time was chosen as June. Constant and time-dependent parameters were considered and sex effects were tested. We assumed that survival did not depend on state, and capture probabilities in both emigrated states were set to zero. We therefore defined 4 parameters (Fig. 3): φ, monthly probability of survival; p, capture probability of individuals in the study area state (not shown in Fig. 3); ε, emigration probability, i.e., transition from study area to newly emigrated state; and ρ, return probability, i.e., transition from emigrated state back to study area.

The models were fitted with the software M-SURGE (Choquet et al. 2004) using sex as an explanatory variable to determine if there were sex-specific survival rates.

Results

Colony size estimates.—The Accra *E. helvum* colony size estimates varied from a maximum of approximately 1 million individuals during the dry season of 2007–2008 to a minimum of approximately 4,000 during the wet season of July 2009, after emigration (Fig. 4). During the 2008–2009 and 2009–2010 dry seasons, the returning migratory population in Accra only reached approximately 250,000–300,000 bats. Seasonal population fluctuations were in synchrony with mean monthly

Table 2.—Competing risk model results for adult survival using senescence and maturation as competing models with constant adult survival. The change in Akaike information criterion (ΔAIC) is the difference between AIC of each model and that of the most parsimonious model; AIC weight summarizes the relative weight of evidence for each model.

Risk model	Log likelihood	ΔAIC	AIC weight
Constant ($l_{x,2}$)	−28.43	0	0.74
Senescence ($l_{x,1}$ $l_{x,2}$)	−28.11	3.4	0.14
Maturation ($l_{x,2}$ $l_{x,3}$)	−28.43	4.0	0.1
Both ($l_{x,1}$ $l_{x,2}$ $l_{x,3}$)	−27.88	6.9	0.02

rainfall, with high population numbers estimated when rainfall was low (data from World Weather Information Service; Fig. 5). In 2008, size of the Tanoboase colony was estimated to be over 3 million individuals, at least 3 times the maximum observed size of the Accra colony.

Age determination.—Histological samples were of good to excellent quality and differential staining between dark cementum annuli and light cementum was good (Fig. 2). Distribution of ages is shown in Fig. 6. Age of most individuals was determined with a margin of error of 1 year, where the annuli either split or merged; however, 3 older animals had an estimated age range from 13 to 15 years. Animals with no annuli were included in the 1-year-old class on the basis of morphometric observations. Birth date was arbitrarily set as 1 March, in line with observations that fetuses from necropsied pregnant females were near term (with a body weight of ~45 g) in March.

Birth rates.—Estimated pregnancy rates (our proxy for birth rates) varied between 0.93 and 0.98 between January and March (Table 1), overall being estimated at 0.96 (95% confidence interval [*CI*] 0.92–0.98). There was no significant variation in proportion of females that were pregnant between capture occasions ($\chi^2 = 1.59$, $d.f. = 2$, $P = 0.45$).

Of 15 female bats euthanized between January and April, 14 were pregnant and the remaining one (sampled in Kumasi) was suckling a pup, which was also euthanized and sampled for virus isolation. Ages of these 15 females, on the basis of tooth cementum annuli, ranged from 1 to 14 years (Fig. 6).

Survival rates.—Of alternative risk models fitted to age frequency data, the one favored by AIC had constant adult survival, with limited support for models including either senescence or maturation of survival rate (Table 2); fit is shown in Fig. 6. Annual adult survival probability, assuming a stationary population size, was estimated to be 0.83 (95% *CI* 0.73–0.93). Mean survival probabilities ranged between 0.79 and 0.87 for different population growth-rate scenarios between $\lambda = -0.05$ (the population decreasing) and $\lambda = 0.05$ (the population increasing), respectively, suggesting moderate sensitivity to the population stability assumption. On the basis of an adult survival probability of 0.83, and 0.48 female births per female (assuming 1:1 birth sex ratio), juvenile survival was estimated to be 0.43, ranging from 0.16 to 0.77 (95% *CI*) when adult survival was varied across its 95% confidence interval.

In CMR analyses of telemetry data, there was strong support for both time and sex effects on recapture and emigration rates, some weaker support for effects of these variables on return rate, and no evidence for any variation in survival rate (Table 3). The 2 top-ranked models, differing only in inclusion of a sex effect on return rate, had a very similar level of support based on AIC (Table 3). Nesting of one within the other allowed use of a likelihood ratio test that determined that the additional sex effect was not statistically significant ($\chi^2 = 2.30$, $P = 0.13$); we therefore selected model M2 as the best of candidate models.

Model M2 has 29 parameters: 1 for survival, 12 for recapture probabilities, 16 for emigration, and 9 for return probabilities. Parameters with both sex and time effects were additive (interaction effects were not supported by AIC). The fitted model resulted in boundary estimates for recapture probability at times 2 and 8 (February and July, respectively). Boundary estimates may in this case be due to low encounter rates and the model may not be able to estimate the parameters away from the boundary. Generally, females had lower recapture probabilities than males, and emigration rates were higher for females than males (although 95% *CI*s overlap considerably, Fig. 4). Maximum likelihood estimates (MLE) for the selected

Table 3.—Top 10 ranked multistate capture–recapture models as selected by Akaike information criterion (AIC), where k is the number of parameters, φ the survival rate, p the recapture probability of individuals in the study area, ε the emigration probability, ρ the return probability (i.e., transition from emigrated state back to study area), g is the sex, t the time (in months), and indicates constant. Additive effects are indicated by +. ΔAIC is the difference between AIC of each model and that of the most parsimonious model; AIC weight summarizes the relative weight of evidence for each model.

Model code	Model	k	Log likehood	ΔAIC	AIC weight
M1	φ(.),p(g+t),ε(g+t),ρ(g+t)	30	−394.682	0.000	0.5
M2	φ(.),p(g+t),ε(g+t),ρ(t)	29	−396.835	0.305	0.43
M3	φ(.),p(g+t),ε(g+t),ρ(g)	22	−412.538	3.712	0.08
M4	φ(.),p(t),ε(g+t),ρ(g+t)	29	−402.793	12.222	0.001
M5	φ(.),p(g+t),ε(t),ρ(g+t)	27	−408.932	16.500	0
M6	φ(g),p(g+t),ε(t),ρ(g+t)	28	−407.826	18.288	0
M7	φ(.),p(g+t),ε(.),ρ(g+t)	23	−418.175	18.986	0
M8	φ(.),p(g+t),ε(g),ρ(g+t)	24	−416.51	19.656	0
M9	φ(g),p(g+t),ε(.),ρ(g+t)	24	−417.167	20.970	0
M10	φ(.),p(g+t),ε(.),ρ(t)	22	−421.422	21.479	0

model's monthly survival probability correspond to an annual adult survival rate of 0.63 (95% *CI* 0.27–0.88, see Appendix III for a summary of MLE for all parameters). Juvenile survival was estimated to range from 0.28 to 1 with estimates from 0.675–0.88, but with adult survival estimates less than 0.675 our assumption of a constant population size ($\lambda = 1$) could not be met.

Movement patterns.—One radiotagged adult male released in Accra in January 2008 was detected by telemetry in Kumasi in November 2008, Accra in December 2008, and in Tanoboase in March 2009. A tagged adult female released in Accra was detected in Tanoboase in March 2009. These findings demonstrate a degree of colony connectivity. Temporal variations in proportion of radiotagged bats detected showed similar patterns over time to those of visual roost counts (Fig. 4).

Discussion

This is the 1st study to estimate demographic parameters from a colony of *E. helvum*, and the 1st to provide estimated adult survival rates for any Pteropodidae. Our observation that on average 96% of breeding females were pregnant matches those estimated in previous studies that describe 1 young per female (Fayenuwo and Halstead 1974; Mutere 1967, 1968). However, pregnancy rates could have been higher, because palpation is likely to be a relatively insensitive method for detection of early pregnancy. Absence of suckling neonates on females caught in Accra (with only 1 exception in Kumasi) and detection of large fetuses by palpation suggest that female *E. helvum* migrate to give birth elsewhere. Timing of pregnancy approximately matched those previously reported in Nigeria and showed strong seasonality. Large mammals usually show slower decline in fecundity from middle age than smaller mammals (Caughley 1977). Bats are particularly long-lived for small-bodied mammals (Barclay and Harder 2003; Turbill et al. 2011) and although our sample size was small, our data (Fig. 6) support the hypothesis that bats may not show this decline in fecundity.

Survival rates are crucial parameters for ecological studies, yet they are difficult to estimate in the field, a task complicated by bat behavior (O'Donnell 2009). The only available report of age-specific survival rates for a Pteropodidae bat (*P. alecto*) was based on forearm length, a technique only useful to age juveniles (Vardon and Tidemann 2000). Such morphological indices are poor predictors of age in adult mammals, and we therefore used canine tooth cementum annuli to estimate age-specific survival rates in *E. helvum*. Clear cementum annuli were visible. The assumption that cementum annuli form only once a year relies on the strong seasonal rainfall pattern in the region and migratory habits of this species. However, this technique, along with use of morphological indices, has a lack of reference standards, such as teeth from animals of known age. Data from captive animals cannot be used with confidence because the lack of cyclical variations in nutritional and environmental factors may affect their growth patterns compared with wild animals (Brunet-Rossini and Wilkinson 2009). This contrast might be even greater in migratory species, such as *E. helvum*, and therefore true cementum deposition rates will only be known once wild animals are marked and teeth analyzed after some known period.

Life table analyses using tooth cementum annuli data provided strong evidence of constant adult survival for *E. helvum* in Ghana. Future analyses with larger sample sizes would help confirm this conclusion (possibly using animals killed for bush meat), and could also determine if extraction of likely less important teeth (such as the first premolar, which may be extracted from living animals) would provide robust results. Varying adult survival within the 0.73–0.93 95% *CI* range has a dramatic effect on estimates of juvenile survival, which ranges from 0.16 to 0.77, assuming a constant population size. Lower estimates from our CMR study suggest that either the population is in decline (see below), or adult survival must be greater than approximately 0.675 for the population to be stable ($\lambda = 1$) given the low birth rate. Therefore our estimate for juvenile survival should be viewed with caution. As mentioned in the introduction, in long-lived animals population growth rates are more sensitive to adult than to juvenile survival (e.g., Lande 1988; Lebreton and Clobert 1990; Saether and Bakke 2000; Gaillard and Yoccoz 2003), and therefore juvenile survival may be less important for harvest models. Recent analysis of insectivorous *Eptesicus fuscus* populations in North America, however, suggests that juvenile survival is important for population survival (George et al. 2011). Future studies should aim to improve both juvenile and adult survival estimates for demographic analyses.

The dramatic reduction in size of the Accra colony between dry seasons of 2007–2008 and 2008–2009 meant that standard CJS CMR models were confounded by heterogeneity in recapture probability. Our multistate model of emigration allowed us to address this. The best-fitting model had constant adult survival, also shown by the cementum annuli analysis. Although confidence intervals for adult survival estimates from the 2 methods overlap (0.83, 95% *CI* 0.73–0.93 for age frequency analysis versus 0.63, 95% *CI* 0.27–0.88 for CMR analysis), estimates are substantially different. If the population is actually declining, life table analyses will overestimate annual survival. This species has reportedly been declining from numerous locations (Mickleburgh et al. 2008; Monadjem et al. 2007), and is subject to substantial bush meat harvesting (Kamins et al. 2011; Mickleburgh et al. 2009). To match the life table survival estimate to that from the CMR analysis, however, it would be necessary to assume a population multiplication rate of 0.75 (25% annual decline), which is a fairly extreme rate of decline. In contrast, the CMR survival estimate is likely to include an element of permanent emigration, thereby underestimating survival. We expect that the true current survival rate probably lies somewhere between these 2 estimates.

For comparison with other bat species, recent analyses of a 25-year, multisite data set have revealed survival rates to vary between sites for a species of European bat (*Eptesicus*

isabellinus—Papadatou et al. 2011), with estimates varying between 0.58 (95% *CI* 0.23–0.92) and 0.81 (95% *CI* 0.73–0.88). This and estimates from other studies (e.g., Frick et al. 2007; O'Shea et al., 2004; Papadatou et al. 2009; Pryde et al. 2005; Schaub et al. 2007; Schorcht et al. 2009) are consistent with our survival estimates for *E. helvum*, although life histories of these species are likely quite different from *E. helvum*. However, colony connectivity and heterogeneity that may affect survival rates should be studied in the future. In particular, effort should be made to determine if age or sex distributions differ between colonies and if those colonies subject to heavy harvesting have altered survival rates.

Taken together, relatively high and constant adult survival rates along with birth rates estimated in this study are consistent with studies that report bats to be similar to larger-bodied mammals with respect to life span and litter sizes (Barclay and Harder 2003; O'Donnell 2009). These results suggest that *E. helvum* could be susceptible to overharvesting, especially given large numbers killed in southern Ghana (Kamins et al. 2011).

Population size is an important variable, not only for conservation (larger populations are more robust) but also for spread and maintenance of infectious diseases, where a critical community size may exist that allows infections to persist (Lloyd-Smith et al. 2005). In Accra, as in other studies (Mutere 1966, 1980; Sorensen and Halberg 2001; Thomas 1983), *E. helvum* colony size was shown to vary dramatically during the year, from up to 1 million individuals to a small nonmigratory population in the wet season. However, the driver of this migratory pattern is still not well understood (Richter and Cumming 2006, 2008). Our observations in Accra are consistent with rainfall-driven seasonality suggested by studies in Ivory Coast (Thomas 1983).

Thomas (1983) reported small, transitory *E. helvum* colonies in Mali, over 1,500 km north of Ivory Coast, during the wet season when Ivory Coast colonies had declined from approximately 500,000 to a few hundred individuals. The greatest cumulative distance recorded for a single *E. helvum* tracked by satellite telemetry was 2,518 km in 149 days (Richter and Cumming 2008). Therefore, the Accra colony may not only be part of a large Ghanaian population, but may be connected to other populations in West and Central Africa. In our study we noted that the Tanoboase colony was very large when the Accra colony was still large (approximately 1 million bats). Thus, it is possible that a large number of absent bats in Accra in 2009 and 2010 moved to this colony, which according to local reports has been increasing in size over the last decade. Future studies should aim to identify destinations of bats emigrating from Ghana using telemetry techniques. Unraveling the full scale of bat migratory movements would help us understand drivers of these migrations and enable us to monitor dynamics of bats and their infections at the metapopulation level.

Our CMR analysis provides evidence that males are less likely to migrate than females (Table 3; Fig. 4), posing interesting questions regarding social structure and costs of migration on reproductive success. Social structure may also be an important factor in the context of infection dynamics because of its effect on contact rates.

Our radiotelemetry data suggest that bats do not always return to the same roost daily. Also, we detected 2 animals (first captured in Accra) in 2 other colonies (Kumasi and Tanoboase) approximately 200 and 300 km from Accra, respectively. *Eidolon helvum* has been monitored by satellite telemetry flying greater distances than these in a single night (Richter and Cumming 2008). One individual adult male tagged in Accra that had migrated was subsequently detected the next dry season in Kumasi, Accra, and then Tanoboase colonies. This demonstrates that at least some individuals use multiple roosts.

In Accra, careful roost counts were used to estimate colony size and our colony count data were corroborated by our radiotelemetry data that showed a similar trend to population count estimates. Causes of the dramatic reduction in the number of bats returning to Accra during the dry seasons of 2008–2009 and 2009–2010 are unknown. Other Pteropodidae have been shown to be highly mobile and show a range of movement behaviors, including nomadism (Breed et al. 2010; Epstein et al. 2009; Howard 1960); this study highlights the potential lack of roost fidelity shown by *E. helvum*. Only long-term monitoring will determine if this is a permanent, temporary, or a cyclical change to the Accra colony size. Long-term population estimates are also required to determine if harvesting rates are currently sustainable.

Interestingly, presence of the large Tanoboase colony has not been previously recorded. Discussions with local people suggest that the colony has substantially increased in size over the last decade. This highlights lack of knowledge of this species, even in a relatively small, well-studied country such as Ghana. From 2007 to 2010, 4 very large colonies (Wli Falls, up to 250,000; Kumasi, up to 500,000; Tanoboase, up to several million; and Accra, up to 1 million) were visited. An additional large dry-season *E. helvum* colony on an island in Lake Volta has also recently been recorded after responses to bush-meat hunter questionnaires (Kamins et al. 2011). Although high mobility of *E. helvum* means that these counts cannot be simply summed to give a reliable estimate of the total population, it is clear that the dry-season *E. helvum* population in Ghana numbers in the millions of bats.

Estimates of population size changes, and of the survival and birth rates, will facilitate future analyses of infection dynamics within the *E. helvum* population in Ghana. *Eidolon helvum* is widespread across sub-Saharan Africa, has a large population size, migrates, and is likely an important seed disperser and plant pollinator in African tropical forest systems (Andriafidison et al. 2006; Picot et al. 2007). Although population numbers appear large, the species is also subject to substantial bush-meat harvesting in West Africa (Mickleburgh et al. 2009). Obtaining estimates for demographic parameters is therefore essential for future analyses of population viability and harvesting sustainability.

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Appendix I

Goodness-of-fit tests: Results of the goodness-of-fit tests in U-CARE (Choquet et al., 2009), to test the fit of the Cormack–Jolly–Seber model to the telemetry data.

Test	χ^2	*d.f.*	*P*
3.SR	3.77	1	0.05
3.SM	0.77	2	0.76
2.CT	132.40	9	0.00
2.CL	5.87	9	0.75
Total	142.81	21	0.00

Appendix II

In Appendix I it is shown that the only significant test is test 2.CT, which is primarily a test for recapture heterogeneity. The test examines whether individuals captured at occasion t_i are more or less likely to be captured at occasion t_{i+1}. We can partition the test statistic in Appendix I into encounter occasion tests and these are displayed. CT numbers 2 through 10 correspond to encounter occasions February 2008 through November 2008.

Test	χ^2	*d.f.*	*P*
2.CT(2)	3.05	1	0.08
2.CT(3)	0.59	1	0.44
2.CT(4)	9.89	1	0.00
2.CT(5)	30.86	1	0.00
2.CT(6)	22.94	1	0.00
2.CT(7)	25.95	1	0.00
2.CT(8)	19.17	1	0.00
2.CT(9)	12.39	1	0.00
2.CT(10)	7.57	1	0.01
2.CT	132.40	9	0.00

From this, we see that individuals captured at occasion 3 or later were more/less likely to be captured on the next occasion. Signed tests indicate that they were in fact less likely to be captured. However, capture probabilities were high due to the use of radio telemetry, and therefore this significant capture heterogeneity could be due to individuals leaving the study area for a period of time, before returning at a later date. If the individuals did not return they would be identified as transients, and would be confirmed by a significant test 3.SR, which is not the case here.

Appendix III

Maximum likelihood estimates (MLE) survival (φ); capture probability of individuals in the study area (p); emigration probability (ε); and return probability (ρ) from model M2 in the manuscript (see Fig. 3 for model structure). *** indicates that a boundary estimate has been obtained. Male (M) and female (F) MLE are shown when estimated.

Parameter	MLE	Lower bound 95% *CI*	Upper bound 95% *CI*
φ	0.962	0.898	0.986
pM(2)	***	***	***
pM(3)	0.892	0.693	0.968
pM(4)	0.784	0.592	0.901
pM(5)	0.859	0.610	0.959
pM(6)	0.925	0.600	0.990
pM(7)	0.923	0.761	0.978
pM(8)	***	***	***
pM(9)	0.982	0.859	0.998
pM(10)	0.990	0.912	0.999
pM(11)	0.984	0.910	0.997
pM(12)	0.983	0.826	0.999
pF(2)	***	***	***
pF(3)	0.512	0.286	0.733
pF(4)	0.316	0.121	0.606
pF(5)	0.436	0.095	0.851
pF(6)	0.610	0.084	0.964
pF(7)	0.605	0.269	0.865
pF(8)	***	***	***
pF(9)	0.873	0.494	0.980
pF(10)	0.927	0.630	0.989
pF(11)	0.885	0.639	0.971
pF(12)	0.878	0.450	0.984
εM(1)	0.062	0.026	0.141
εM(2)	0.079	0.012	0.379
εM(3)	0.377	0.233	0.545
εM(4)	0.253	0.092	0.529
εM(5)	0.258	0.111	0.492
εM(6)	0.157	0.054	0.379
εF(1)	0.066	0.023	0.176
εF(2)	0.084	0.013	0.400
εF(3)	0.393	0.147	0.708
εF(4)	0.266	0.050	0.712
εF(5)	0.271	0.087	0.592
εF(6)	0.166	0.043	0.469
ρ(3)	***	***	***
ρ(4)	0.531	0.034	0.974
ρ(5)	0.057	0.006	0.381
ρ(6)	0.062	0.002	0.715
ρ(7)	0.089	0.024	0.280
ρ(8)	0.282	0.139	0.488
ρ(9)	0.292	0.118	0.559
ρ(10)	0.240	0.066	0.587
ρ(11)	0.248	0.050	0.674