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Change-in-ratio density estimator for feral pigs is less biased than closed mark–recapture estimates

Laura B. Hanson[A,E], *James B. Grand*[B], *Michael S. Mitchell*[C], *D. Buck Jolley*[A], *Bill D. Sparklin*[D] *and Stephen S. Ditchkoff*[A]

[A]School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA.
[B]US Geological Survey, Alabama Cooperative Wildlife Research Unit, Auburn University, Auburn, AL 36849, USA.
[C]US Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812, USA.
[D]Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812, USA.
[E]Corresponding author. Email: laurabhanson@hotmail.com

Abstract. Closed-population capture–mark–recapture (CMR) methods can produce biased density estimates for species with low or heterogeneous detection probabilities. In an attempt to address such biases, we developed a density-estimation method based on the change in ratio (CIR) of survival between two populations where survival, calculated using an open-population CMR model, is known to differ. We used our method to estimate density for a feral pig (*Sus scrofa*) population on Fort Benning, Georgia, USA. To assess its validity, we compared it to an estimate of the minimum density of pigs known to be alive and two estimates based on closed-population CMR models. Comparison of the density estimates revealed that the CIR estimator produced a density estimate with low precision that was reasonable with respect to minimum known density. By contrast, density point estimates using the closed-population CMR models were less than the minimum known density, consistent with biases created by low and heterogeneous capture probabilities for species like feral pigs that may occur in low density or are difficult to capture. Our CIR density estimator may be useful for tracking broad-scale, long-term changes in species, such as large cats, for which closed CMR models are unlikely to work.

Introduction

Estimating population density (i.e. abundance per unit area) of wild animals is a common goal in wildlife research and management. The density of feral pigs (*Sus scrofa*) is of interest to researchers and land managers because where they are an invasive species, they are considered economic and environmental pests (Kotanen 1995; Dickson *et al*. 2001; Hone 2002). Density has been the population measure of choice to determine the extent of a feral pig problem and the success of population reduction efforts (Coblentz and Baber 1987; Choquenot *et al*. 1997; Hone 2002).

Abundance is often estimated using closed capture–mark–recapture (CMR) methods that incorporate detection probabilities (Williams *et al*. 2002). However, low detection probabilities and heterogeneity caused by time, behaviour or differences between individuals can lead to negatively biased estimates (Williams *et al*. 2002; Link 2003). Sources of heterogeneity add cumulatively to bias an abundance estimate (Chen and Lloyd 2000). Information specific to individual animals can be used to reduce bias owing to individual heterogeneity, but only if the information explains differences in detection probabilities among individuals (Huggins 1989; Alho 1990). Although the majority of feral pig studies have used an index to estimate density (Woodall 1983; Saunders and Giles 1995; Choquenot *et al*. 1997; Hone 2002), the few studies that used closed CMR methods found that feral pigs generally have low and heterogeneous detection probabilities (Baber and Coblentz 1986; Coblentz and Baber 1987; Caley 1993).

Density estimation methods other than closed CMR are needed for species like feral pigs that are difficult to capture or have unmeasured or unmeasurable traits that affect detection probability. We developed a density estimator, D_{CIR}, based on the change in the ratio (CIR) of survival rates between two populations; our estimator used open CMR models to estimate survival (Barker 1997; White and Burnham 1999), thus reducing the bias of heterogeneous detection probabilities associated with closed CMR estimation methods. Traditionally, CIR methods have been used on a single population sampled for catch-per-unit effort before and after removal (Williams *et al*. 2002). We designed D_{CIR} to evaluate a change in survival rates between two separate populations, one of which was subjected to removal of individuals.

We used D_{CIR} to estimate the density of feral pigs on Fort Benning, Georgia, USA in 2004. We calculated the estimate for a portion of Fort Benning where survival of pigs from 2004 to 2005 was representative for the base (control), by comparing them to survival rates in an area where pigs were subjected to intensive removal (treatment). To evaluate D_{CIR}, we compared its estimate

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to a minimum density estimate, based on the minimum known number of pigs alive (D_{MIN}), and two estimates generated by closed-population CMR models (D_{CLOSE_HUG} and D_{CLOSE_CHAO}) for the same year.

Materials and methods

Study area

Our research was conducted between spring (May) 2004 and autumn (August) 2005 at the Fort Benning Military Reservation in west-central Georgia, USA (32°21′N, 84°58′W). The 737-km^2 military base was located on the Coastal Plain–Piedmont Fall Line with elevations ranging from ~50 to 230 m. The climate was semitropical with an average annual rainfall of 132 cm (Dilustro *et al.* 2002); average maximum temperatures in July and January were 33.2°C and 13.8°C, respectively. Fort Benning was dominated by stands of longleaf pine (*Pinus palustris*), loblolly pine (*Pinus taeda*), shortleaf pine (*Pinus echinata*) and scrub oak species (*Quercus* spp.) in the uplands. Riparian bottomlands consisted of yellow poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), hickory (*Carya* spp.), ash (*Fraxinus* spp.) and oak species (King *et al.* 1998). Our research was conducted in two 50-km^2 areas (control and treatment), located ~8 km apart and separated by a river, therefore assumed to be independent. Hunting of feral pigs occurred year-round in both study areas.

Capture–mark–recapture

Trapping and handling

We conducted 18-day trapping sessions during each summer, 2004 and 2005, in the control and treatment areas using 20 spring-loaded cage traps (capable of catching multiple pigs) spaced 1–2 km apart in each area. We tagged all captured pigs with uniquely numbered ear tags in both ears (National Band and Tag, Newport, KY). A ratio of head length to body length was used to estimate age, assuming this relationship holds for all feral pigs (Boreham 1981). We recorded sex and estimated weight based on dead pigs with known weights. We used Telazol (Fort Dodge Animal Health, Fort Dodge, IA; 1 cc per 30 kg) to sedate selected adult females and attached a global positioning system (GPS) collar (Advanced Telemetry Systems, Isanti, MN). We monitored collared pigs weekly for mortality via radiotelemetry (using very high frequency (VHF) signals, before collar retrieval and downloading of GPS locations). Handling of all pigs was conducted in accordance with institutional animal care and use guidelines of Auburn University (PRN# 2003-0531).

Camera recapture

We used digital game cameras (infrared Digital-Scout 3.2 mega pixel; Penn's Woods, Export, PA, USA) to resample ear-tagged feral pigs between the 2004 and 2005 trapping sessions. In each study area, we used 16 cameras rotated every 2–3 weeks among sites baited with fermented corn, spaced 1–2 km apart to achieve even coverage. We set cameras with a 2-min delay between exposures to acquire multiple photographs of visiting groups, which assisted with identification.

Closed-population CMR estimates

We used both the Huggins (Huggins 1989) closed-capture model (Program MARK) and Chao's estimator (Chao 1988; Program CAPTURE) to acquire closed CMR abundance estimates in the control area for 2004. The Huggins model allowed us to model detection probabilities using individual covariates including sex, age, estimated weight and observed weather conditions. Program CAPTURE used estimated detection probabilities, but cannot incorporate individual covariates to generate abundance estimates.

Survival estimation

We used the CMR Barker model in Program MARK, which incorporates live captures, live resights (e.g. camera resightings and telemetry locations of live animals) and dead recoveries (Barker 1997; White and Burnham 1999) to estimate apparent survival of all pigs $\geq$1 month old in each of the control and treatment areas (Hanson 2006).

Minimum known number of pigs alive

We calculated the minimum number of pigs known to be alive in the control area as the total number of pigs caught in traps plus the total number of identifiable, untrapped individuals sighted by cameras during late summer and early autumn. Untagged individuals were identified by their unique colour and markings. We assumed pigs sighted by cameras through early autumn were likely in the population during the summer because reproduction was not documented until November.

Effective sampling area

To calculate density (pigs km^{-2}) for the control area in 2004, we estimated total effective sampling area (A_E) with 95% confidence intervals (CI) by creating buffers around each trap in 2004. Buffer distance equalled half the average longest straight-line distance pigs moved during the length of a trapping session (d_L). We estimated d_L from GPS locations of collared sows using the Animal Movement extension in ArcView 3.2 (Hooge and Eichenlaub 1997). We used ArcView to create buffers based on d_L around trap locations and summed the area of nonoverlapping buffers to represent A_E. We calculated 95% CI for A_E based on buffers defined using the upper and lower confidence limits for d_L.

Density estimation

We estimated abundance for the control area in 2004 by dividing the total number of pigs removed from the treatment area by the percentage by which survival was reduced in the treatment population compared with the control population. This method assumes that survival rates were equal in the control and treatment populations before the experimental removal efforts and that both populations experienced the same environmental conditions. We divided abundance estimates by the effective sampling area to estimate density:

$$D_{CIR} = (N_H/\Delta S)/A_E$$

where N_H = number of pigs removed from the treatment area, ΔS = percentage reduction in survival between the control and treatment areas and A_E = effective sampling area for the control area. We calculated the 95% CI for D_{CIR} ad hoc by dividing the lower and upper 95% CI for survival by the lower and upper 95% CI for A_E, respectively.

We estimated minimum density for the control area in 2004 as:

$$D_{MIN} = MKNA/A_E$$

where MKNA = the minimum number of pigs known to be alive in the control area. We calculated 95% confidence limits on D_{MIN} using the lower and upper 95% CI for A_E.

We estimated density for the control in 2004 using the closed population CMR models as:

$$D_{CLOSE\_HUG} = \widehat{N}/A_E$$

where $\widehat{N}$ = the population estimated using the Huggins model in Program MARK and

$$D_{CLOSE\_CHAO} = \widehat{N}/A_E$$

where $\widehat{N}$ = the population estimated using the Chao estimator in Program CAPTURE.

We divided abundance estimates by the effective sampling area to estimate density. We calculated the CI for the density estimates ad hoc by dividing the lower and upper 95% CI for $\widehat{N}$ by the lower and upper 95% CI for A_E, respectively.

Results

Capture–mark–recapture

During the two 18-day control area trapping sessions in 2004, we caught 64 pigs and recaptured 53.1%. In 2005, we caught 62 pigs in the control area with a recapture rate of 40.3%. Cameras in the control area recorded >4200 photographs over 10 months, with resightings of trapped pigs occurring in 35% of the photographs. No pigs from the treatment area were ever recaptured, resighted or reported dead in the control area, or vice versa, supporting our assumption about independence of the populations.

Closed-population CMR estimates and MKNA

The top-ranked Huggins model estimated an initial capture probability ranging from 0.11 to 0.15 and a recapture probability ranging from 0.05 to 0.09, with both depending on prior rainfall. The Huggins model estimated the size of the pig population in the control area in 2004 to be $\widehat{N}$ = 60.2 (95% CI 55.8, 73.8).

The model selection procedure within Program CAPTURE selected M_h as the best model with an estimator, where detection probability varies between individuals. We estimated abundance using Chao's moment estimator, which is the best abundance estimator for species with low detection probabilities and high individual heterogeneity (Chao 1988; Davis *et al*. 2003). Chao's moment estimator for M_h estimated an average detection probability of 0.06, with a range from 0.04 to 0.10. Chao's estimator in Program CAPTURE estimated the size of the pig population in the control area in 2004 to be $\widehat{N}$ = 93.0 (95% CI 74.7, 152.4).

The minimum number of pigs known to be alive in the control area in 2004 was 100, including 64 pigs trapped during the summer and 36 untagged pigs (>3 months old) photographed during early autumn.

Survival estimation

During summer 2004, we captured and tagged a total of 90 pigs from the control and treatment areas. Between August 2004 and May 2005, 39% were resighted using digital game camera photographs, 13% were relocated only via VHF radiotelemetry and ear tags of 31% were returned by hunters. The goodness of fit test using the global model indicated little overdispersion in the data with $\hat{c}$ = 1.15. The Barker model estimated apparent annual survival for all feral pigs older than 1 month to be 0.25 (95% CI 0.19, 0.31) and 0.17 (95% CI 0.10, 0.24) in the control and treatment populations, respectively.

Effective sampling area

We used GPS location data from 12 collared sows during trapping sessions to define buffer distance around each trap sight in the control area in 2004. Half of the average maximum distance moved by collared feral pigs between two points was 1.28 km (95% CI 1.08, 1.48) over any 18-day period, thus we added a 1.28-km (95% CI 1.08, 1.48) buffer around each of 20 trap sites. Area of summed, non-overlapping buffers (A_E) was 51.8 km^2 (95% CI 44.1, 58.6) in 2004.

Density estimation

Between August 2004 and May 2005, 108 feral pigs were experimentally removed from the treatment area. Lethal manipulation resulted in 34.0% (95% CI 24.4, 49.5) lower survival rates in the treatment population compared with the control population. Our estimate of D_{CIR} for the control area in 2004 was 6.13 pigs km^{-2} (95% CI 3.72, 10.04), our estimate of D_{MIN} was 1.92 feral pigs km^{-2} (95% CI 1.70, 2.26), our estimate of D_{CLOSE_HUG} was 1.16 pigs km^{-2} (95% CI 0.95, 1.67) and our estimate of D_{CLOSE_CHAO} was 1.79 pigs km^{-2} (95% CI 1.27, 3.46).

Discussion

Although CMR methods of density estimation based on closed-population models are less biased than indices (Anderson 2001; White 2005), these estimates can still be biased for populations of animals with low or heterogeneous detection probabilities (Williams *et al*. 2002). To avoid these biases, we developed a density estimator based on a change in ratio in survival, calculated using a CMR model for open populations, between a representative population of animals and a population subjected to intensive removal efforts.

We used this model to estimate the density of feral pigs in an area of Fort Benning thought to be representative of the base, by comparing survival estimates there to those estimated for a portion of the base subjected to intensive removal of pigs. Feral pigs had a very low probability of being captured in traps, and detection probabilities often differed between individuals for unknown reasons (Baber and Coblentz 1986; Coblentz and Baber 1987; Caley 1993), creating the potential for biased density estimates calculated using closed CMR methods.

The D_{CIR} estimator addresses closed CMR and traditional change-in-ratio biases associated with heterogeneous detection probabilities by using the open CMR Barker model, which is more robust to heterogeneity in detection probabilities (Williams *et al*. 2002), to estimate survival. However, the D_{CIR} estimate could be biased if the two populations were not identical in structure before the removal efforts and did not experience the same environmental events. The D_{CIR} estimator also requires the robust estimation of effective sampling area in order to calculate density. We chose to use actual distances moved by pigs during the closed sampling period instead of using estimates of home-range size because observed individuals may not cover their entire home range during sampling; in this case, use of home-range area could bias D_{CIR} low. Studies lacking home-range data will often use half the estimated mean maximum distance moved between camera trap sites as the buffer distance, which can lead to an overestimate in density (Soisalo and Cavalcanti 2006; Dillon and Kelly 2008). Additionally, our buffer distance of 1.28 km is comparable to the 0.9–1.5 km distance radio-collared pigs moved to consume bait in Australia (McIlroy *et al*. 1993).

Consistent with our expectations that low and heterogeneous capture probabilities in a feral pig population could influence a density estimate from a closed-population CMR model, D_{CLOSE_HUG} and D_{CLOSE_CHAO} produced unrealistic point estimates that were less than the known minimum density of pigs known, D_{MIN}, for the control area in 2004. By contrast, D_{CIR} reflects an estimate appropriately exceeding the minimum. We did not test, however, the extent to which D_{CIR} is an unbiased estimate of density. Comparison of D_{CIR} estimates to known populations would be needed to evaluate its accuracy. Based on our ad hoc calculations of CI, precision of D_{CIR} was not high, suggesting it may not be appropriate for tracking small changes in density over time, or slight differences in density between populations. Some of the imprecision in our D_{CIR} estimates is likely due to the relative paucity of data used to estimate survival for our pig populations.

The D_{CIR} method may be a useful CMR approach to estimating density of manipulated or exploited wildlife populations characterised by low and heterogeneous capture probabilities (e.g. large carnivores), and where individuals are removed from at least one portion of the population, and survival rates are known. Compared with closed-population CMR methods, using an open-population model with D_{CIR} can require less-intensive sampling efforts but longer sampling periods. A potential downfall associated with long sampling periods is that density estimates are averaged over a period of time where the population may be fluctuating in size, thus obscuring patterns in density over finer time scales. Thus, D_{CIR} may be most useful for tracking broad-scale, general trends, and has the potential for doing so more accurately than estimators using closed CMR models when capture probabilities are low and heterogeneous.

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