

Sperm competition drives the evolution of suicidal reproduction in mammals

Diana O. Fisher^{a,1}, Christopher R. Dickman^b, Menna E. Jones^c, and Simon P. Blomberg^a

^aSchool of Biological Sciences, University of Queensland, St Lucia, QLD 4072, Australia; ^bInstitute of Wildlife Research, School of Biological Sciences, University of Sydney, Sydney, NSW 2006, Australia; and ^cSchool of Biological Sciences, University of Tasmania, Hobart, TAS 7001, Australia

Edited by James H. Brown, University of New Mexico, Albuquerque, NM, and approved August 29, 2013 (received for review June 5, 2013)

Suicidal reproduction (semelparity) has evolved in only four genera of mammals. In these insectivorous marsupials, all males die after mating, when failure of the corticosteroid feedback mechanism elevates stress hormone levels during the mating season and causes lethal immune system collapse (die-off). We quantitatively test and resolve the evolutionary causes of this surprising and extreme life history strategy. We show that as marsupial predators in Australia, South America, and Papua New Guinea diversified into higher latitudes, seasonal predictability in abundance of their arthropod prey increased in multiple habitats. More-predictable prey peaks were associated with shorter annual breeding seasons, consistent with the suggestion that females accrue fitness benefits by timing peak energy demands of reproduction to coincide with maximum food abundance. We demonstrate that short mating seasons intensified reproductive competition between males, increasing male energy investment in copulations and reducing male postmating survival. However, predictability of annual prey cycles alone does not explain suicidal reproduction, because unlike insect abundance, peak ovulation dates in semelparous species are often synchronized to the day among years, triggered by a species-specific rate of change of photoperiod. Among species with low postmating male survival, we show that those with suicidal reproduction have shorter mating seasons and larger testes relative to body size. This indicates that lethal effort is adaptive in males because females escalate sperm competition by further shortening and synchronizing the annual mating period and mating promiscuously. We conclude that precopulatory sexual selection by females favored the evolution of suicidal reproduction in mammals.

Dasyuridae | Didelphidae | life history trade off | seasonality | senescence

Semelparity in both sexes occurs in many plants and invertebrates and in some fish. In these taxa, conditions that produce low adult survival between breeding bouts, but high juvenile survival to reproductive maturity select for semelparity, provided that high enough fecundity can evolve to compensate for reduced lifespan (1). Obligate maternal care means that mammals are constrained to a relatively low maximum reproductive rate. This should generally preclude the evolution of semelparity in mammals (2, 3). However, the maximum reproductive rate of males is much less constrained than that of females. In species with large litters such as insectivorous marsupials (4), males with low or zero postreproductive survivorship can potentially compensate by siring many offspring among multiple females in their first reproductive bout (5), so that divergence in life history strategies between the sexes can be favored by a mechanism of sexual selection.

The adaptiveness of male die-off in marsupials has been debated without resolution for three decades (2–4, 6, 7). We propose that to understand why male semelparity has evolved in mammals, we must answer two separate questions: (i) why has evolution favored males that compete fatally in these marsupial species but not in other mammals and (ii) what mechanism of sexual competition facilitates this lethal effort only in males? Five potential reasons why insectivorous marsupials are prone to

evolve lethal male competition have been proposed: (i) females are constrained to leave a 12-mo gap between litters because a peak in arthropod prey occurs annually in their seasonally predictable forest habitats, weaning success depends on this spike in food, and females have a long lactation time relative to body size (a marsupial trait). Environmental causes of mortality (rife in small mammals) mean that adult males of these species seldom survive for a year after maturity, and lethal competition in the first season is adaptive because males are unlikely to breed again (Braithwaite and Lee's hypothesis) (2); (ii) phylogenetic predisposition (an unknown developmental constraint locking modern taxa into nonadaptive male die-off) (7); (iii) accumulation of deleterious mutations after breeding (6); (iv) poor survival of breeding females resulting in male bet-hedging (spreading the risk of offspring death among many mates) and therefore extreme male promiscuity (8); or (v) altruism (males sacrificing themselves to avoid competing with the next generation for limited food) (2, 3, 9). Braithwaite and Lee's adaptive framework, based on the exceptional lactation time of dasyurids, is the only one of these suggestions to address why die-off has not evolved more widely in small mammals. This hypothesis was based on the traits of a small number of forest-dwelling species (2) and has been criticized because prey cycles appear to be less synchronized between years than the reproductive cycles of semelparous mammals (9). However, habitat and latitudinal effects on seasonality of insect abundance have not been quantified at continental scales, and dasyurid species with die-off occur in diverse, nonforest habitats (7, 10).

Alternative explanations have proposed that peculiarities of the mating system lead to extreme sexual selection and that this is sufficient reason for the evolution of mammalian semelparity. Most forms of sexual selection have been proposed as the mechanism of competition in dasyurids with die-off: male contests that

Significance

In some marsupial genera but in no other mammals, escalating stress hormones during the breeding season cause immune system collapse and synchronized death after mating in all males (suicidal reproduction). In this paper, we resolve the environmental drivers and adaptive mechanism of sexual selection responsible for the repeated evolution of this surprising and extreme life history strategy in mammals. The strategy of synchronized suicidal reproduction in mammals resulting in male death before offspring are born has often been attributed to altruistic or kin-selected paternal suicide to avoid food depletion. We show that rather than altruism or kin-selection, individual sexual selection leads to apparent self-sacrifice in these genera.

Author contributions: D.O.F. designed research; D.O.F., C.R.D., and M.E.J. performed research; S.P.B. analyzed data; and D.O.F., C.R.D., M.E.J., and S.P.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

See Commentary on page 17610.

¹To whom correspondence should be addressed. E-mail: d.fisher@uq.edu.au.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1310691110/-DCSupplemental.

favor young males (2, 6), precopulatory female preference for young males (6), female choice in the form of lekking (selection for male endurance through metabolism of muscle) (11), and sperm competition (4). Of these, only sperm competition has empirical support (5). Precopulatory fighting is infrequent and minor in male semelparous marsupials (12). In the semelparous genus *Antechinus*, mating females reject subordinate males but are indifferent to male body size and mate promiscuously with most available males (12–14), suggesting that even if there was variation in male age, youthfulness would not motivate mate choice. Lekking occurs in some populations of only one species, if at all (11, 15). In contrast, there is rigorous evidence of the importance of sperm competition in semelparous species (4, 5, 14). In the brown antechinus *Antechinus stuartii*, sperm competition enables females to improve offspring survival and lifetime fitness by mating promiscuously (5). Here we use phylogenetic comparative methods to test the predictions of these competing hypotheses to explain why, among mammals, male semelparity has evolved repeatedly (10) and only in insectivorous marsupials, and to determine whether die-off is likely to have evolved through a mechanism of sperm competition.

Life history variation has previously been treated as discrete life history categories in evolutionary investigations of dasyurid marsupials (10), but demographic studies of insectivorous marsupials in Australia, South America, and Papua New Guinea reveal a continuum (7, 16–18). The most extreme strategy (die-off) involves a set of peculiar physiological events that culminate in synchronous death: males irreversibly shut down sperm production a month before mating so that future reproduction is impossible. Fertilization depends on sperm stored in the epididymis, and males continuously lose sperm in the urine (spermatorrhea) so that the window of opportunity to mate before permanent infertility is very brief. Synchronous immune system collapse and death quickly follow. Die-off occurs in all males of the Australian genera *Antechinus* (12 species), *Phascogale* (3 species), and *Dasykaluta* (a monospecific genus) (10). One species in each of two other genera in Australia is “facultatively semelparous”; only some populations have complete male mortality. Die-off symptoms of immune collapse and abrupt, synchronous death occur in semelparous populations of the dibbler *Parantechinus apicalis*, but not the northern quoll *Dasyurus hallucatus* (7, 16). Some Brazilian, Argentinean, and Australian small marsupials also have negligible survival after breeding at some sites (17–19) (Table S1). This phenomenon in didelphid mouse opossums occurs in both sexes and has been termed “partial semelparity” (18). Most insectivorous dasyurids and didelphids are iteroparous (repeat or continuous breeding, at the

other extreme of the scale), including all known species in Papua New Guinea (Table S1).

Results

We tested whether the seasonal predictability of prey is greatest in high latitude forest habitats (2) by calculating Colwell's index of seasonal predictability (P) for arthropod prey at sites inhabited by dasyurids (20) (Table S2). By testing correlates of arthropod seasonality at a continental scale, we show that prey seasonality increases with latitude (Fig. 1 and Fig. S1; $r = 0.38$, $F_{1,3} = 7.8$, $P = 0.01$) and is greater in grassland than in forest or rainforest (Fig. 1; $F_{1,3} = 8.2$, $P = 0.003$). Sampled species occurred in a relatively narrow range of latitudes in forest and shrubland habitats (Fig. S2), but in a wider latitudinal range in grassland and rainforest, where prey seasonality increases linearly with distance from the equator (Fig. 1 and Fig. S1).

The mean index of seasonal prey predictability (P) was negatively associated with the breeding season length of species occurring at sites where prey were sampled [Bayesian regression coefficient, -1.33 ; SD, 0.57 ; 95% highest posterior density (HPD) interval, -2.45 to -0.018 ; 95% central posterior density (CPD) interval, -2.45 to -0.20 ; Fig. 2]. The last month of lactation or month of weaning was the month of mean peak prey abundance in all monestrous species. The most common weaning month was December, and the most common month of peak prey abundance was January (Table S3). In insectivorous marsupials, taxa with shorter breeding seasons had lower postmating survival of males (Bayesian regression coefficient, 7.3 ; SD, 1.8 ; 95% HPD interval, 3.9 – 11.0 ; 95% CPD interval, 4.0 – 11.3 ; $n = 52$). Male reproductive effort in the form of sperm competition is associated with mating duration and testes size in mammals (21–23). Insectivorous marsupial taxa with lower postmating survival of males had much longer mean copulation durations (9.4 ± 0.8 vs. 3.7 ± 0.5 h), indicating relatively greater energy expenditure per mating (Table 1). To examine why males evolved an inability to breed again and lost the flexibility to extend the mating season beyond a very brief time (rather than simply evolving reduced survival at the expense of sperm competition success within a season), we focused on taxa with $<10\%$ postcopulatory survival in males. In these species, those with die-off had larger testes in relation to body size (Fig. 3 and Table 1) and shorter breeding seasons (Fig. 2 and Table 1).

Discussion

In agreement with predictions of one aspect of Braithwaite and Lee's hypothesis (2), that the long lactation time and diet of insectivorous marsupials constrain females to synchronize

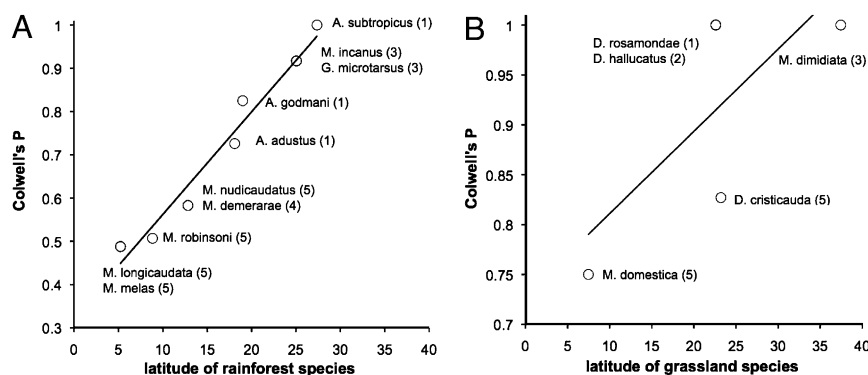


Fig. 1. Mean index of seasonal predictability in arthropod abundance (Colwell's P) plotted against mean latitude of sample points for 10 species of dasyurid and didelphid marsupials in rainforest habitats (A) and 5 species in grassland (B). $P = 1$ if there is complete between-year predictability in the months of peak arthropod abundance. Numbers in parentheses are ranks of iteroparity in males: (1) die-off, (2) facultative semelparity, (3) $<1\%$ survival between cohorts, no die-off, (4) 1–10% survival between cohorts, (5) iteroparity.

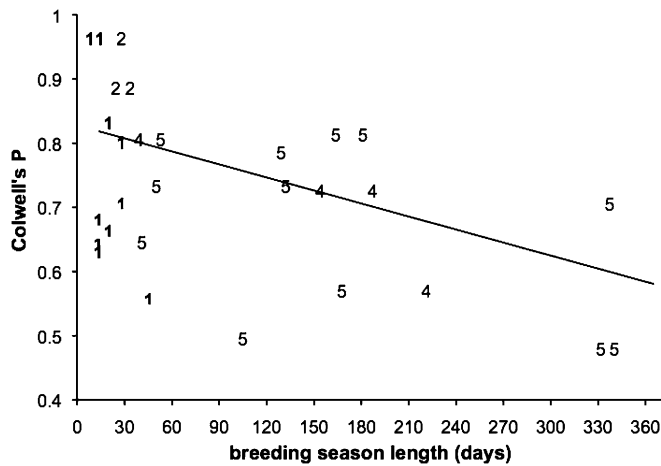


Fig. 2. Mean Colwell index of seasonal predictability in arthropod abundance (P) at sites with population studies or surveys of insectivorous marsupials, plotted against breeding season length of each species (number of days of the year on which mating can occur, determined at the same sites; $n = 31$). The line indicates the fitted linear regression. Numbers show iteroparity rank of males of each species (1 = die-off, 5 = iteroparity). Species with shorter breeding seasons occur at sites with higher values of P on average.

breeding with the prey peak in seasonal habitats, seasonal prey predictability is negatively associated with breeding season length (Fig. 2), and late lactation and weaning (times of peak maternal energy demand and mortality risk for offspring) coincide with peak prey abundance in all monestrous species (Table S3). Ancestral dasyurids and didelphids were probably iteroparous, seasonal breeders (10), so this suggests that females shortened the mating period to synchronize weaning with the month of peak prey abundance when they diversified into highly seasonal southern regions (not only in forests) and lengthened the breeding season when they speciated in the tropics (10).

Short periods of population-wide female sexual receptivity are expected to intensify male competition, because individual males cannot monopolize a series of females but must compete at the same time if estrus is synchronous across a population (22, 24). In our analyses, taxa with shorter breeding seasons had lower postmating survival of males. This suggests that in species with shortened breeding seasons as a result of strong prey seasonality (Fig. 2), competition has increased at the expense of postmating

survival in males. Morphological and behavioral indicators suggest that male contests are likely to be predominantly through sperm competition. Testis size increases relative to body size in response to risk of sperm competition in mammals (22, 23), and individuals with larger testes have greater fertilization success in competitive matings in many species, including the semelparous dasyurid *Antechinus* (13, 21, 22). Increased sperm competition is also associated with longer copulations in mammals, because this behavior can block rival males from displacing or diluting sperm (21). Species with die-off have larger testes in relation to body size and shorter breeding seasons than species with low postmating survival but no synchronous immune collapse. This supports the hypothesis that foregoing the flexibility to extend the mating period and sire young in repeated breeding seasons gives males an advantage in sperm competition (11). Thus, in the most extreme cases of *Antechinus*, *Phascogale*, and *Dasykaluta*, in which females have maximized sperm competition among males by highly synchronizing estrus and mating promiscuously, the die-off mechanism is adaptive in males even though the resulting immune collapse is fatal.

An adaptive hypothesis to explain why insectivorous marsupials are prone to evolve lethal male competition is strongly supported by our comparative data. There is therefore no need to invoke nonadaptive developmental constraints (7). Phylogenetic predisposition to accumulate deleterious mutations after breeding (6) is also an unlikely explanation because this predicts that accelerated female senescence is associated with the evolution of semelparity (6). In fact, male and female post-reproductive survival are not correlated (in dasyurids: $F_{1,42} = 0.46$, $P = 0.94$, $r = 0.07$), which directly contradicts the hypothesis that poor survival of breeding females influences the evolution of male die-off because it causes extreme male promiscuity (8). Although one of the elements of Braithwaite and Lee's explanation is supported by our analyses (long lactation interacting with prey seasonality), the others are not. The relatively high adult female survival rate in species with relatively high male semelparity, and the lack of die-off in very small species (Fig. 3) both contradict their suggestion that die-off is favored because males in species prone to evolve semelparity are unlikely to survive to a second breeding season due to extrinsic mortality causes, even if they lack the physiological mechanism of synchronized death (2).

Multiple authors have proposed that male die-off benefits offspring by reducing competition for food, as a complete or partial explanation for the propensity of insectivorous marsupials to evolve lethal male competition (2, 3, 9). We reject this as implausible, because it invokes group selection [no benefit to

Table 1. Correlates of male life history strategy in insectivorous marsupials

Variable	Coefficient	SD	95% highest posterior density interval	95% central posterior density interval
Intercept*	18.69	10.75	(-2.39, 39.77)	(-1.61, 40.66)
Copulation duration*	-1.39	0.69	(-2.76, -0.09)	(-2.88, -0.18) [†]
Scrotal width*	-0.57	0.76	(-2.07, 0.92)	(-2.09, 0.91)
Body mass*	0.04	0.05	(-0.05, 0.14)	(-0.05, 0.14)
Scrotal width:body mass*	-0.001	0.002	(-0.005, 0.002)	(-0.004, 0.002)
Intercept [‡]	-74.88	43.33	(-161.18, -5.22)	(-177.63, -12.0) [†]
Breeding season length [‡]	-0.13	0.09	(-0.32, -0.004)	(-0.37, -0.02) [†]
Scrotal width [‡]	4.82	3.04	(-0.23, 10.82)	(0.31, 11.89)
Body mass [‡]	22.29	11.58	(3.38, 45.04)	(5.47, 49.81) [†]
Scrotal width:body mass [‡]	-1.35	0.76	(-2.85, -0.10)	(-3.17, -0.24) [†]

*Bayesian cumulative logistic regression mixed model with the dependent variable male iteroparity rank (52 species). Species with longer copulations have lower postmating survival of males.

[†]Significant associations.

[‡]Bayesian logistic regression model with the dependent variable low (<10%, above zero) vs. zero male survivorship between seasons (1 = die-off, 0 = no die-off; 26 species). In these species, male die-off is associated with a shorter breeding season, greater scrotal width in relation to body mass, and greater body mass.

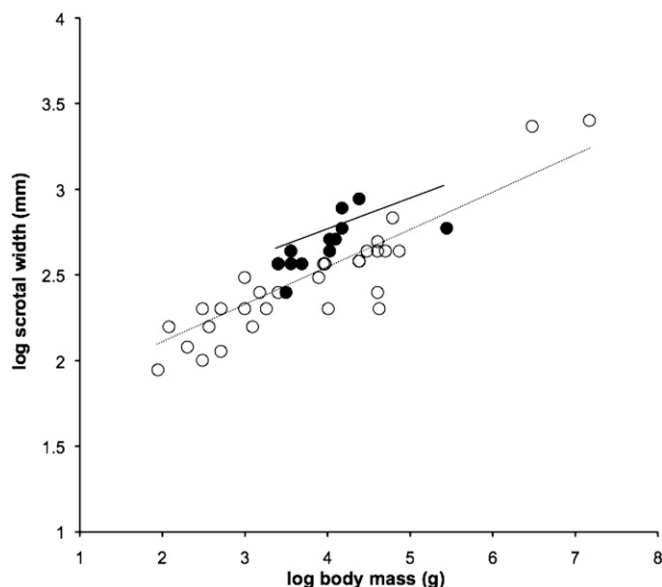


Fig. 3. Mean scrotal width plotted against body mass of male insectivorous marsupials with <10% postmating survival in males (iteroparity ranks 1, 2, 3, and 4) on a log scale ($n = 44$). Filled points indicate species with die-off (rank 1). The dashed line indicates the fitted linear regression for species with <10% postmating survival in males, and the solid line is for species with die-off.

individual males, which sire offspring with many females but are often outside these females' usual home ranges (11)] and assumes that summer food shortage causes weight loss in *Antechinus* in late lactation (9). However, tradeoffs in maternal allocation cause maternal weight loss, which is unrelated to competition for food. Prey availability is not limiting in summer and mothers still lose weight if given unrestricted food in captivity (25).

Strong sexual divergence in reproductive lifespan also occurs in some spiders, in which sexual selection has led to adaptive suicidal reproduction in males of at least one species because cannibalized males manipulate female behavior to increase paternity (26). We propose that in semelparous marsupials, females manipulate male behavior to increase their own reproductive success. Males in seasonally predictable habitats increase mating effort at the expense of survival, not because adult male or female survival is low for environmental reasons in these habitats (which are relatively benign and predictable) or because males are altruistic, but ultimately because females profit from sperm competition (5). Environmental seasonality sets the scene for females to impose severe sexual selection pressure on males by shortening the breeding period and mating with extreme promiscuity (5, 14).

Materials and Methods

Data. We collated published life history data on insectivorous marsupials in Australia, Papua New Guinea, and South America (Tables S1–S4). We ranked degree of semelparity in males of 52 species as follows: (i) die-off, i.e., corticosteroid feedback system failure and irreversible disintegration of the testes followed by spermatorrhoea, so that males rely on a finite supply of stored sperm during their one mating season, the mating period is very short, male death is synchronized and a second breeding season is impossible (occurring in 25% of insectivorous marsupial species in our dataset: ~20% of genera); (ii) facultative semelparity (die-off in some populations); (iii) <1% survival between cohorts, no die-off, male mortality is unsynchronized; (iv) 1–10% survival between cohorts; and (v) iteroparity. We estimated female postbreeding survival as the mean proportion of second-season (or older) females recorded in the breeding period. We defined breeding season length of each species at the population level, as the number of days of the year on which mating can occur. Breeding seasons fell into three discrete categories with respect to potential predictors (see below) (2–8, 16–34, and 52 wk).

Seasonal Predictability of Prey Abundance. We calculated seasonal predictability of prey based on multiyear studies reporting monthly arthropod abundance at sites with captures of insectivorous marsupials ($n = 22$). For these species, life history data are predominantly from studies at these sites. For each study, we categorized monthly abundances as high (top 25% of abundances) or low (lower 75% of abundances) to calculate Colwell's index (P) (20). We omitted seldom-eaten taxa (ants, collembola) (27).

Colwell's index (P) uses categorical data. P is a measure of how tightly an event is linked to a season. It is composed of C = constancy, a measure of how uniformly the event occurs across all seasons ($C = 1$ if the frequency is the same in all seasons), and M = contingency, a measure of the repeatability of seasonal patterns ($M = 1$ if abundance is the same every summer, autumn, winter, and spring, but different between seasons, for example). We calculated mean P for sites in which marsupial species occurred ($n = 31$ species).

Predictability (P) is the sum of constancy and contingency (20). In a contingency table with t columns (months within an annual cycle) and s rows (abundance category states), X_j refers to column totals, Y_i to row totals, Z to grand totals, and H to uncertainty (see worked example in ref. 20).

$$P = 1 - H(XY) - H(X)/\log s, \text{ where}$$

$$H(X) = - \sum_{j=1}^t \frac{X_j}{Z} \log \frac{X_j}{Z}$$

and

$$H(XY) = - \sum_i \sum_j \frac{N_{ij}}{Z} \log \frac{N_{ij}}{Z}$$

Bayesian Regression Methods. We used Bayesian mixed-effects cumulative logistic regression models in R (28, 29) to test the following three predictions, incorporating phylogenetic information (Fig. S3) as random effects. (i) Prey predictability is correlated with breeding season length. The breeding schedule data were discontinuous with respect to prey predictability (P), so we tested if P differs between species with three ranked categories of breeding season length: short (2–8 wk), medium (16–34 wk), and long (52 wk) ($n = 31$ species). (ii) Male iteroparity rank depends on breeding season length (in the above three categories) ($n = 52$ species). (iii) Traits indicating sperm competition intensity: copulation duration, (log) body mass, scrotal width, or an interaction between (log) body mass, and scrotal width, are correlated with male iteroparity rank ($n = 52$ species). We used a Bayesian mixed-effects binomial logistic regression model in R (28, 30) to test whether breeding season length, (log) body mass, scrotal width, or an interaction between body mass and scrotal width differ between species with <10% postmating male survival that do or do not have male die-off. We did not include the trait of copulation duration in this analysis, because copulation duration has been reported in only three species with <10% postmating male survival that lack die-off.

To account for phylogenetic effects in each model, we added a random effect to the linear predictor for each species. We used a multivariate normal prior for the random effects, with unit variances and correlation structure derived from the phylogenetic tree using Grafen's branch lengths (31). For the covariates, we used diffuse normal prior distributions with zero mean and precision equal to 10^{-6} . To account for missing data (8% of data values), we used separate diffuse Normal priors on each missing data value, as for the covariates. Preprocessing of data was conducted using R version 2.14.0 (28). Markov Chain Monte Carlo analyses were performed in JAGS version 3.1.0 (29), and a burn-in of 100,000 iterations was used, after which 30 million iterations were performed with a thinning rate of 1,000. Three chains were computed, and convergence was checked by eye and by examination of the Geweke and Gelman-Rubin tests (30, 32). Summary statistics were calculated on the pooled chains. The coda package (33) was used for postprocessing, diagnostics, plotting, and calculation of summary statistics.

ACKNOWLEDGMENTS. We thank Alejandro Canepuccia, Juan Pablo Isacch, John Gollan, Mick Ashcroft, Gerry Cassis, Dale Roberts, Pauline Grierson, Mark Harvey, Natalia Leiner, Ric How, Wendy Foster, Luis Verde Arregoitia, Gerhardt Kortner, Lynda Veyret, and Christine Cooper for providing or helping us to locate data, and Marcel Cardillo for comments on the manuscript. D.O.F., C.R.D., and M.E.J. were supported by Australian Research Council Fellowships (DP0773920, FT110100191, DP0988535, FT100100250).

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