

Research



Cite this article: Collett RA, Baker AM, Fisher DO. 2018 Prey productivity and predictability drive different axes of life-history variation in carnivorous marsupials. *Proc. R. Soc. B* **285**: 20181291.

<http://dx.doi.org/10.1098/rspb.2018.1291>

Received: 10 June 2018

Accepted: 10 October 2018

Subject Category:

Evolution

Subject Areas:

ecology, evolution, theoretical biology

Keywords:

Dasyuridae, life history, seasonality, fast–slow continuum, iteroparity, semelparity

Author for correspondence:

Rachael A. Collett

e-mail: rachael.collett@uqconnect.edu.au

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4267451>.

Prey productivity and predictability drive different axes of life-history variation in carnivorous marsupials

Rachael A. Collett¹, Andrew M. Baker² and Diana O. Fisher¹

¹School of Biological Sciences, University of Queensland, Brisbane, Queensland 4072, Australia

²School of Earth, Environmental and Biological Sciences, Queensland University of Technology, Brisbane, Queensland 4000, Australia

RAC, 0000-0002-9727-6622

Variation in life-history strategies has usually been characterized as a single fast–slow continuum of life-history variation, in which mean lifespan increases with age at maturity as reproductive output at each breeding event declines. Analyses of plants and animals suggest that strategies of reproductive timing can vary on an independent axis, with iteroparous species at one extreme and semelparous species at the other. Insectivorous marsupials in the Family Dasyuridae have an unusually wide range of life-history strategies on both purported axes. We test and confirm that reproductive output and degree of iteroparity are independent in females across species. Variation in reproductive output per episode is associated with mean annual rainfall, which predicts food availability. Position on the iteroparity-semelparity axis is not associated with annual rainfall, but species in regions of unpredictable rainfall have longer maximum lifespans, more potential reproductive events per year, and longer breeding seasons. We suggest that these two axes of life-history variation arise because reproductive output is limited by overall food availability, and selection for high offspring survival favours concentrated breeding in seasonal environments. Longer lifespans are favoured when reproductive opportunities are dispersed over longer periods in environments with less predictable food schedules.

1. Introduction

Variation between species in schedules of survival, growth, and reproduction is usually considered on one axis of life-history variation from fast to slow [1–3], assuming that trade-offs between age at maturity, fertility, and lifespan constrain life-history strategies, so that species invest most in either reproduction (faster species) or survival (slower species) [4,5]. However, several analyses have suggested that the degree of iteroparity (i.e. breeding repeatedly in a dispersed time period at one end of the spectrum and breeding once in a concentrated time period at the other) is independent of the fast–slow continuum. That is, the degree of iteroparity (number and spacing of reproductive events) is not necessarily traded off with life-history speed (investment in reproduction versus longevity). Stearns [6] found a secondary precociality–altriciality continuum in mammals after accounting for the slow–fast continuum, and Gaillard *et al.* [7] identified this as part of a semelparity–iteroparity axis that accounts for up to 15% of variation in birds and mammals. In a more recent factor analysis of mammals, Bielby *et al.* [5] identified a factor that explained up to half of the variance between species, and included maturity, weaning time, and time between reproductive bouts. A second factor explained a further quarter of the variance and described output per reproductive episode. Species at one end produced large litters of small young and species at the other end invested more in large but few young. Bielby *et al.* [5] interpreted species position on this output axis in terms of the well-known offspring number versus quality

trade-off, which is grounded in physiological constraints [8,9]. Salguero-Gomez *et al.* [10] have recently also demonstrated that the fast–slow continuum in plants includes traits of growth rate and lifespan on one axis and degree of iteroparity on another. Iteroparity is a risk-spreading reproductive tactic and is likely to be an advantage in variable environments. When conditions favouring offspring survival are unpredictable, bet-hedging by repeated breeding increases fitness, given a trade-off between reproduction and survival [11–13]. Bielby *et al.* [5] called for research to test how the iteroparity and reproductive output axes in mammal life-history variation are associated with environmental variability.

Reproductive output, which includes number and size of offspring, is expected to be constrained by food availability and a female's ability to use energy and nutrients for reproduction [1,14,15]. In marsupial taxa, adoption of higher energy diets has been associated with evolutionary switches to higher reproductive rates. Corresponding trade-offs between reproductive output and other life-history traits have led to the evolution of fast life-history strategies in carnivorous species [16]. Rainfall and temperature seasonality might also influence age-specific survival [17], which determines how species should trade off reproduction and survival [18]. We therefore predict that in carnivorous marsupials from the Family Dasyuridae, which are distributed widely across climate zones, features of climate that increase overall arthropod availability will be correlated with higher reproductive output in terms of litter size per reproductive bout and a faster life history.

Adaptive reproductive timing coincides with events that maximize offspring survival, such as seasonal rainfall and peaks in prey abundance [11,19,20]. For example, the desert chameleon (*Furcifer labordi*) from Madagascar has evolved semelparity and extended incubation time in an arid, seasonal environment [21]. Similarly, Australian dasyurids with late maturity, monoestry and semelparity occur where there are predictable annual peaks in arthropod abundance, because only one favourable time to wean young per year is possible, given that the marsupial trait of long lactation precludes breeding in the season of an individual's birth [22]. We therefore predict that features of climate that increase food seasonality and the predictability of peaks in prey abundance will be correlated with semelparity in female dasyurids.

Using databases of life-history traits (see the electronic supplementary material for source references), location records in the Australian marsupial Family Dasyuridae, and long-term climate data, we test how female reproductive output, degree of iteroparity, and lifespan covary with food abundance and seasonal predictability of food.

(a) Specific predictions

We hypothesise that reproductive output and degree of iteroparity in females are independent: output will depend on food availability and not food predictability, whereas degree of iteroparity will depend on food predictability and not food availability. We therefore predict that litter size and the number of neonates at birth will covary with the amount of rainfall, and lifespan, length of the annual reproductive season, and the number of reproductive attempts will covary with rainfall predictability.

2. Methods

(a) Study taxa

Dasyurids are predominantly insectivorous, range in size from less than 5 g to 9 kg, and have a maximum lifespan of 1–6 years [23]. The maximum number of young that can be reared is determined by the number of teats, which vary from two to 14. Some groups such as antechinus produce supernumerary young: they give birth to more young than the number of teats, so some inevitably die at birth. Other species produce fewer young than the number of teats [24]. In seasonal breeders, the reproductive season lasts for two weeks to six months, depending on the species. Uniquely in mammals, dasyurid males include the entire spectrum from obligate semelparity to iteroparity. Females can breed multiple times and vary from virtually semelparous to continuous breeding [16,18,25]. Complete male die-off occurs in 20% of dasyurid species (Fisher *et al.* [22]), including: all in the genera *Antechinus*, *Phascogale*, and *Dasykaluta* [26]; *Dasyurus* and *Parantechinus* each contain a single species with facultatively semelparous males [27,28]. Females from some species are monoestrous (i.e. breed once a year), while others are polyoestrous (i.e. can produce multiple litters per season) [29].

(b) Data

We collated published female life-history data on 34 Australian dasyurids taken from 82 studies (table 1; electronic supplementary material). We only included species that are predominantly insectivorous (arthropods are greater than 75% of their diet), because associations between rainfall and arthropod availability have been quantified [22], allowing us to use rainfall as a proxy for food availability [30]. Traits analysed included: body mass at adulthood, maximum lifespan, polyestry versus monoestry, duration of reproductive season (indicating number of possible reproductive attempts), litter size, and number of supernumerary young. Where possible, we used published field studies. Because potential within-breeding episode trade-offs with short-term food supply are likely to be important in dasyurids [30], we used offspring number per reproductive bout rather than a ratio of long-term output over time such as reproductive rate. We used litter sizes recorded within a week of birth, because mothers may progressively lose pouch young during lactation. We calculated mean values for traits when there were multiple studies of the same species. We defined the duration of the reproductive season as the number of weeks with births [31].

We used rainfall as a proxy for arthropod availability (abundance and activity) [32]. For each species, we used mean annual rainfall at the centroid of geographical range based on all recorded locations [22]. We calculated seasonal predictability of rainfall by collating monthly rainfall from the Bureau of Meteorology [33] at the study sites where life-history information was collected. We gathered these data for the 10 years preceding the end of the study, as Fisher *et al.* [22] found that 3–8 years of insect and climate data gave repeatable results and clear outcomes in tests of hypotheses at these sites. For each site, we categorized monthly rainfall as 'high' if it was in the top 25% of abundances, or 'low' if it was in the lower 75% of abundances. We used these categorical data to calculate a Colwell index for rainfall at each site where marsupial life-history data were collected [22]. Colwell's index (*P*) uses categorical data to measure how tightly an event is linked to a season. *P* is composed of *C* (constancy) and *M* (contingency). Constancy describes how uniform the event is across seasons. Contingency measures the repeatability of seasonal patterns between years. *P* is maximized when the event occurs constantly throughout the year or if the pattern of occurrence is repeated across years [34].

Table 1. Dasyurid species included in this study and the number of published studies data was collated from. PTR (personal trapping records) and PC (personal correspondence).

Species	No. of studies
<i>Antechinomys laniger</i>	2
<i>Antechinus agilis</i>	1 and PTR
<i>Antechinus bellus</i>	2
<i>Antechinus flavipes</i>	3 and PTR
<i>Antechinus godmani</i>	1 and PTR
<i>Antechinus leo</i>	2
<i>Antechinus minimus</i>	3
<i>Antechinus stuartii</i>	1 and PTR
<i>Antechinus subtropicus</i>	PTR
<i>Antechinus mimetes</i>	2
<i>Dasycercus cristicauda</i>	PC
<i>Dasykaluta rosamondae</i>	3
<i>Dasyuroides byrnei</i>	2
<i>Dasyurus hallucatus</i>	3
<i>Dasyurus viverrinus</i>	2
<i>Ningai ridei</i>	3
<i>Parantechinus apicalis</i>	3
<i>Parantechinus bilarni</i>	3
<i>Phascogale calura</i>	2
<i>Phascogale tapoatafa</i>	4
<i>Planigale gilesi</i>	3
<i>Planigale ingrami</i>	3
<i>Planigale maculata</i>	2
<i>Planigale tenuirostris</i>	3
<i>Pseudantechinus macdonnellensis</i>	2
<i>Pseudantechinus ningbing</i>	1
<i>Sminthopsis crassicaudata</i>	4
<i>Sminthopsis douglasi</i>	1
<i>Sminthopsis griseoventer</i>	1 and PC
<i>Sminthopsis leucopus</i>	3
<i>Sminthopsis macroura</i>	4
<i>Sminthopsis murina</i>	2
<i>Sminthopsis ooldea</i>	2
<i>Sminthopsis virginiae</i>	2

(c) Statistical analyses

We log-transformed body mass, lifespan, and length of the reproductive season and arcsin-transformed rainfall predictability (P) to normalize the distributions [35]. We used phylogenetic generalized least-squares (PGLS) models in R, using the packages *ape* [36] and *nlme* [37] to test the relationships between predictor variables: annual rainfall, rainfall predictability (P), lifespan, length of the reproductive season, and polyestry, and response variables: lifespan, length of the reproductive season, litter size, and supernumerary young, incorporating phylogenetic information and body mass into models. We used a recent marsupial phylogeny [38] to account for interspecific autocorrelation due to phylogeny [39]. We used a multivariate normal prior for the phylogenetic random effects, with unit variances

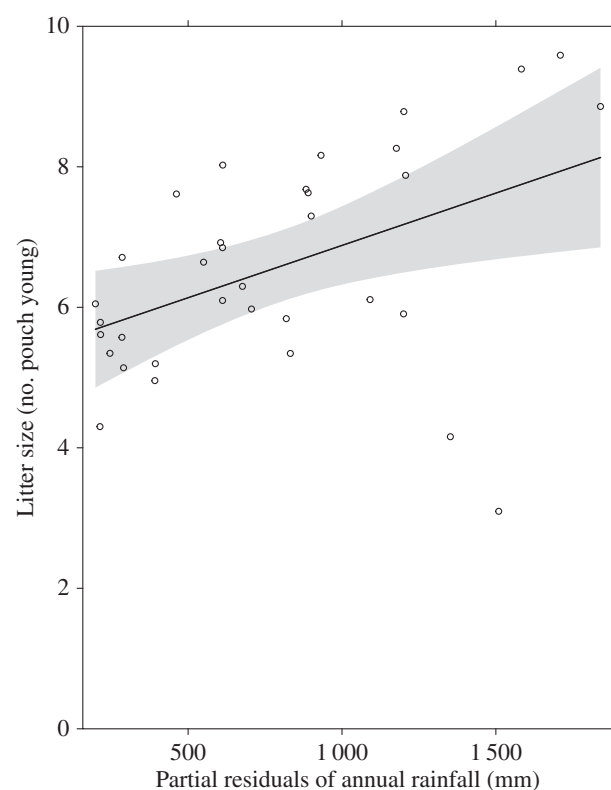


Figure 1. The association between litter size and partial residuals of mean annual rainfall for Australian insectivorous dasyurid species. The line indicates the fitted regression from model one, including 95% confidence intervals.

and correlation structure derived from the phylogenetic tree using Grafen's branch lengths [40]. We calculated a pseudo *r*-squared for each PGLS model [41].

3. Results

(a) Trade-offs and climate predictors of reproductive output

In agreement with our hypothesis that food availability limits reproductive output, species in more arid climates produced fewer young per reproductive bout (litter size versus mean annual rainfall: $t = 2.72$, $p = 0.01$, d.f. = 34, slope = 0.001, s.e. = 0.0005; figure 1). Litter size was negatively associated with mass ($t = -2.89$, $p = 0.007$, d.f. = 34, slope = -0.68 , s.e. = 0.24). Species with larger litters were more likely to have supernumerary young ($t = 3.47$, $p = 0.002$, d.f. = 34, slope = 1.64, s.e. = 0.47), and the number of supernumerary young was correlated with annual rainfall ($t = 2.14$, $p = 0.04$, d.f. = 34, slope = 358, s.e. = 167), further supporting our prediction that there would be a positive relationship between food availability and reproductive output. Species occurring in Australia's arid and semi-arid zones (less than 350 mm annual rainfall) never had more than seven young, and only one desert species, the kowari (*Dasyuroides byrnei*), produced any supernumerary young. In agreement with our prediction that reproductive output would not vary with food predictability, litter size was not significantly related to P (rainfall predictability) ($t = -0.4$, $p = 0.69$, d.f. = 34, slope = -0.79 , s.e. = 2) (pseudo *r*-squared for model one = 0.32). Litter size was also not associated with traits that indicate the degree of iteroparity in females (litter size versus length of reproductive season: $t = -1.85$,

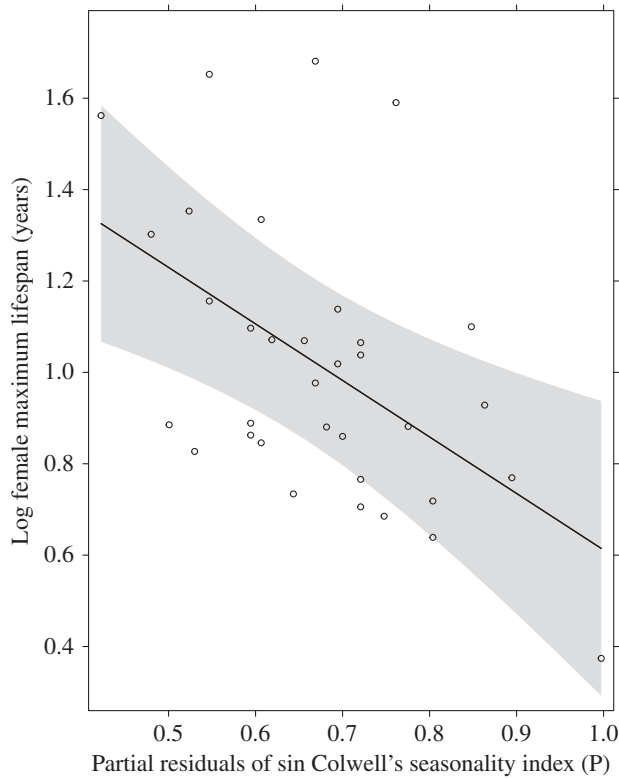


Figure 2. The association between log female maximum lifespan and partial residuals of sin Colwell's predictability index of rainfall for Australian insectivorous dasyurid species. The line indicates the fitted regression from model three, including 95% confidence intervals.

$p = 0.07$, d.f. = 34, slope = -0.08 , s.e. = 0.04 ; litter size versus polyestry: $t = 1.19$, $p = 0.24$, d.f. = 34, slope = 1.1 , s.e. = 0.92) and dasyurids do not trade off litter size against lifespan (litter size versus lifespan: $t = -0.04$, $p = 0.97$, d.f. = 34, slope = -0.04 , s.e. = 1.03) (pseudo r -squared for model two = 0.25). Litter size of species in our study ranged from four to 10.

(b) Trade-offs and climate predictors of the degree of iteroparity

Female maximum lifespan of species in our study ranged from one to six years and were positively associated with mass ($t = 2.27$, $p = 0.03$, slope = 0.11 , s.e. = 0.05). As predicted, lifespan was longer in areas with more unpredictable food supplies (lifespan versus rainfall predictability index P: $t = -3.23$, $p = 0.003$, d.f. = 34, slope = 1.24 , s.e. = 0.38 , figure 2) (pseudo r -squared for model three = 0.32). Species with long lifespans are more likely to have long reproductive seasons (lifespan versus reproductive season length: $t = 4.29$, $p = 0.0002$, d.f. = 34, slope = 0.02 , s.e. = 0.005) (pseudo r -squared for model four = 0.38) and to have multiple litters per season (lifespan versus polyestry: $t = 2.51$, $p = 0.02$, d.f. = 34, slope = 0.25 , s.e. = 0.1) (pseudo r -squared for model five = 0.19). Reproductive season length alone was also strongly associated with rainfall predictability (reproductive season length versus rainfall predictability index P: $t = -4.73$, $p = 0.0001$, d.f. = 34, slope = -0.89 , s.e. = 0.26 , figure 3) (pseudo r -squared for model six = 0.14). This supports our hypothesis that adaptation to a seasonal climate, and therefore predictability of food schedules, favours a short reproductive period in

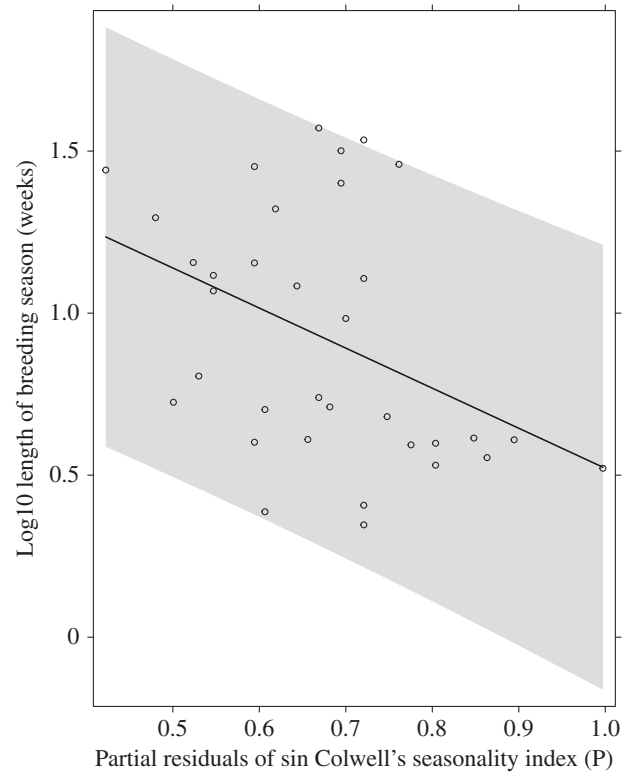


Figure 3. The association between log10 length of the breeding season and partial residuals of sin Colwell's predictability index of rainfall for Australian insectivorous dasyurid species. The line indicates the fitted regression from model six, including 95% confidence intervals.

seasonal environments, and a long lifespan with repeat breeding over a long period is more likely to evolve where there is less predictable rainfall. Annual rainfall did not significantly predict rainfall predictability ($t = 1.14$, $p = 0.26$, d.f. = 32, slope = 731 , s.e. = 643.1), as some regions of arid Australia where dasyurids were sampled have highly predictable rainfall, and some more mesic areas have unpredictable rainfall (figure 4). For example, *Ningaui timealeyi* (body weight 5.8 g) has a maximum lifespan of one year, and although its Western Australia Pilbara location is a dry environment, summer cyclones are common and most annual rainfalls predictably in February [43]. *Planigale gilesi* (body weight 6.9 g) in arid western New South Wales is similar in size and ecology but lives for a maximum of five years in a region where low, annual rainfall falls unpredictably across the year [44].

4. Discussion

Our results agree with several previous analyses, which concluded that aspects of the fast-slow continuum are independent of the semelparity-iteroparity axis in mammals. We focused on offspring number, because previous studies revealing multiple axes of life-history variation in mammals identified reproductive output as a key variable [5,7]. The theory basis of within-bout trade-offs with litter size is well established [15,45]. Experiments and descriptive tests in small eutherian mammals have shown that the trade-off between the number and prenatal growth rate of offspring in a litter is strongly affected by physiological constraints of energy, nutrients, temperature, and tissue capacity. Total

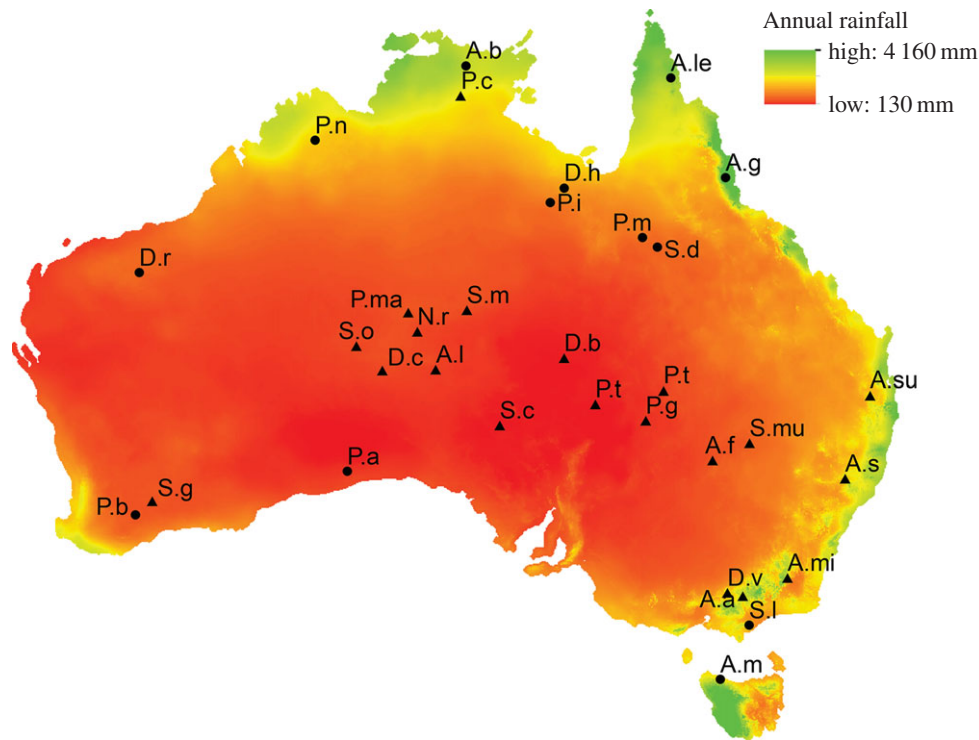


Figure 4. The centroid point of the geographical range of dasyurid species included in this study and mean annual rainfall throughout Australia. Species are marked with a Δ if Colwell's P is less than 0.7 (less seasonally predictable) and a \circ if Colwell's P is equal to or more than 0.7 (more seasonally predictable). For full species names see table 1. Rainfall raster data were taken from Reside *et al.* [42].

investment in reproduction is expected to reduce long-term survival under the disposable soma theory, which states that investment in reproduction reduces individual somatic maintenance [46,47]. In an environment with high extrinsic mortality in adults, organisms should invest in early and high reproductive output rather than long-term maintenance and survival. Position of a species on the fast–slow continuum is therefore expected to depend on aspects of its ecology and environment that affect age-specific mortality risk [48]. Litter size and growth is traded off within each reproductive episode based on maternal investment capacity at the time [9,15]. However, distributing this investment over a longer breeding period does not necessarily change the upper limit on the number of offspring per litter. For example, rate of milk transfer and heat production are mechanisms limiting investment within a reproductive bout [15,45]. Habitats and ecology that cause higher extrinsic mortality risk do not necessarily have higher or lower seasonal predictability of food. If they do, the direction of selection can be reversed. For example, Reznick *et al.* [49] found that guppies in high predation sites evolved faster reproduction when high predation environments had scarcer food, perhaps because predators indirectly reduced net mortality by reducing density and thus competition for food. In variable environments, organisms that hedge their bets by dispersing reproductive effort over a longer breeding season and have a longer reproductive lifespan have a lower risk of failure [11,45]. Orzack & Tuljapurkar [50] showed that unpredictable environments could favour either high or low reproductive output through their effect on reproductive costs.

In our study, rainfall seasonality was unrelated to annual rainfall. Therefore, aspects of the environment that affect whether iteroparity or semelparity is likely to lead to greater fitness in females are at least partly disconnected from aspects of the environment that affect whether females can

invest in large litters and whether mortality risk and reproductive costs are likely to lead to higher fitness in females that increase reproductive effort.

As predicted, a climate variable related to the predictability of peaks in prey abundance (rainfall predictability) was correlated with species position on the semelparity–iteroparity axis, and a variable that alters food availability and reflects energy limitation (annual rainfall) was associated with variation in reproductive output. These findings concord with some previous predictions in mammals and other vertebrates. For example, in the mammal family Leporidae (rabbits and hares) temperature seasonality predicted 71% of the global variation in litter size and body size, and the authors interpreted this in terms of food limitation caused by seasonality. Unpredictable timing of stressful environmental conditions was associated with increased iteroparity, whereas nest predation rate predicted 55% of variation in the timing trait of gestation duration [19]. In endemic mammal families in Madagascar, iteroparity involving short intervals between breeding episodes, a long breeding season, and high adult survival is common, and this has been attributed to the particularly unpredictable timing of rainfall on this island [11]. Comparing desert populations of a ground squirrel on a gradient of increasing seasonal predictability, Whorley [20] also found that more unpredictable rainfall was associated with longer breeding seasons, lower synchrony, and smaller litter size. In Rose's mountain toadlet (*Capensibufo rosei*), 94% of variation in toad lifespan between years is explained by variation in breeding season rainfall. In dry years, survival is increased and reproductive output is low, and in wet years, toads increase reproduction at the expense of survival [51].

In dasyurids, we found that species with large litters were more likely to occur in high rainfall habitats and to have supernumerary births. Arid zone species rarely had

supernumerary young and often failed to have all teats occupied by neonates, suggesting they cannot reliably obtain enough food to produce excess young. We conclude that energy or nutrient availability constrains female reproductive output, consistent with many studies of limitations to reproductive output in small mammals (e.g. [16,52–58]. For example, Sibly & Brown [58] found that mass of mammal neonate tissue was associated with reliable and abundant food. However, seasonality is often also associated with reproductive output, because seasonal environments have a reliable annual pulse of abundant food, especially at high latitudes. For example, offspring number often increases with environmental seasonality in birds [59,60] and mammals, including European lagomorphs [19], boars (*Sus scrofa*) [61], and ground squirrels (*Ammospermophilus leucurus*) [20]. Similar trends have not been obvious in carnivorous and Southern Hemisphere mammals at lower latitudes [62,63], with the exception of *Antechinus agilis* in the relatively low latitude of southern Australia [64]. Unlike seasonal Australian environments, Northern Hemisphere habitats with severe winters have large seasonal peaks in food availability relative to the scarcest season [59].

We found that degree of iteroparity in female dasyurids across the continent was correlated with predictability of rainfall and thus schedules of reliable food availability. Species in environments with seasonally predictable rainfall were more likely to be monoestrous, have shorter lifespans, and shorter reproductive seasons. These species time reproduction so that late lactation, which is energetically costly [56], coincides with the peak in arthropod availability [22]. Female dasyurids in regions of unpredictable rainfall live longer, are more likely to be polyestrous, and have longer reproductive

seasons. The opportunity for multiple breeding attempts over several years is likely to be adaptive if survival of young is highly variable [12,65], as a long reproductive period enables bet-hedging, which increases the likelihood of some births during times of high food availability [66]. Bet-hedging strategies occur in plants (desert annuals) [13], bees (*Perdita portalis*) [67], tortoises (*Gopherus agassizii*) [68], primates [66], and many other taxa, which spread their reproductive effort over multiple episodes in unpredictable environments [65,69].

Patterns of rainfall explained significant variation in production of young, lifespan, and length of the reproductive season. However, there was still a large proportion of variance unexplained by our models. These effects might be mediated by competition and population density [70], temperature [45], rates of age-specific predation [49,71–73], and torpor [74], which would be promising future avenues for further understanding of the mechanisms.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. R.A.C. and D.O.F. created the database. R.A.C. performed the analyses. R.A.C., D.O.F., and A.M.B. contributed to the manuscript. All the authors gave their final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. This research is supported by the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub and an Australian Research Council fellowship, Grant/Award no. FT110100191.

Acknowledgements. We thank Simon Blomberg for assistance with R scripting and April Reside for assistance with mapping.

References

- Brown JH, Sibly RM. 2006 Life-history evolution under a production constraint. *Proc. Natl Acad. Sci. USA* **103**, 17 595–17 599. (doi:10.1073/pnas.0608522103)
- Harvey PH. 1989 Life history variation in placental mammals: unifying the data with theory. *Oxf. Surv. Evol. Biol.* **6**, 13–31.
- Gaillard J-M, Lemaître J-F, Berger V, Bonenfant C, Devillard S, Douhard M, Gamelon M, Plard F, Lebreton J-D. 2016 Life Histories, Axes of Variation. In *Encyclopedia of evolutionary biology*, vol. 2 (ed. RM Kliman), pp. 312–323. Oxford: Academic Press.
- Oli MK. 2004 The fast–slow continuum and mammalian life-history patterns: an empirical evaluation. *Basic Appl. Ecol.* **5**, 449–463. (doi:10.1016/j.baae.2004.06.002)
- Bielby J, Mace GM, Bininda-Emonds OR, Cardillo M, Gittleman JL, Jones KE, Orme CD, Purvis A. 2007 The fast-slow continuum in mammalian life history: an empirical reevaluation. *Am. Nat.* **169**, 748–757.
- Stearns SC. 1983 The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* **41**, 173–187. (doi:10.2307/3544261)
- Gaillard J-M, Pontier D, Allaine D, Lebreton J, Trouvilliez J, Clobert J. 1989 An analysis of demographic tactics in birds and mammals. *Oikos* **56**, 59–76. (doi:10.2307/3566088)
- Smith CC, Fretwell SD. 1974 The optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506. (doi:10.1086/282929)
- Rollinson N, Hutchings JA. 2013 Environmental quality predicts optimal egg size in the wild. *Am. Nat.* **182**, 76–90. (doi:10.1086/670648)
- Salguero-Gómez R, Jones OR, Jongejans E, Blomberg SP, Hodgson DJ, Mbeau-Ache C, Zuidema PA, de Kroon H, Buckley YM. 2016 Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proc. Natl Acad. Sci. USA* **113**, 230–235. (doi:10.1073/pnas.1506215112)
- Dewar RE, Richard AF. 2007 Evolution in the hypervariable environment of Madagascar. *Proc. Natl Acad. Sci. USA* **104**, 13 723–13 727. (doi:10.1073/pnas.0704346104)
- Stearns SC. 1992 *The evolution of life histories*. Oxford: Oxford University Press.
- Venable DL. 2007 Bet hedging in a guild of desert annuals. *Ecology* **88**, 1086–1090. (doi:10.1890/06-1495)
- Sibly RM, Brown JH. 2009 Mammal reproductive strategies driven by offspring mortality-size relationships. *Am. Nat.* **173**, E185–EE99. (doi:10.1086/598680)
- Król E, Johnson M, Speakman J. 2003 Limits to sustained energy intake VIII. Resting metabolic rate and organ morphology of laboratory mice lactating at thermoneutrality. *J. Exp. Biol.* **206**, 4283–4291. (doi:10.1242/jeb.00676)
- Fisher DO, Owens IP, Johnson CN. 2001 The ecological basis of life history variation in marsupials. *Ecology* **82**, 3531–3540. (doi:10.1890/0012-9658(2001)082[3531:TEBOLH]2.0.CO;2)
- Ellis BJ, Figueredo AJ, Brumbach BH, Schlomer GL. 2009 Fundamental dimensions of environmental risk. *Human Nat.* **20**, 204–268. (doi:10.1007/s12110-009-9063-7)
- Ricklefs RE. 2010 Life-history connections to rates of aging in terrestrial vertebrates. *Proc. Natl Acad. Sci. USA* **107**, 10 314–10 319. (doi:10.1073/pnas.1005862107)
- Virgos E, Cabezas-Díaz S, Blanco-Aguilar JA. 2006 Evolution of life history traits in Leporidae: a test of nest predation and seasonality hypotheses. *Biol. J. Linnean Soc.* **88**, 603–610. (doi:10.1111/j.1095-8312.2006.00646.x)
- Whorley JR, Kenagy G. 2007 Variation in reproductive patterns of antelope ground squirrels, *Ammospermophilus leucurus*, from Oregon to Baja

- California. *J. Mammal.* **88**, 1404–1411. (doi:10.1644/06-MAMM-A-382R.1)
21. Karsten KB, Andriamandimbiasoa LN, Fox SF, Raxworthy CJ. 2008 A unique life history among tetrapods: an annual chameleon living mostly as an egg. *Proc. Natl Acad. Sci. USA* **105**, 8980–8984. (doi:10.1073/pnas.0802468105)
 22. Fisher DO, Dickman CR, Jones ME, Blomberg SP. 2013 Sperm competition drives the evolution of suicidal reproduction in mammals. *Proc. Natl Acad. Sci. USA* **110**, 17 910–17 914. (doi:10.1073/pnas.1310691110)
 23. Van Dyck S, Gynther I, Baker A. 2013 *Field companion to the mammals of Australia*. Sydney, N.S.W.: New Holland Publishers.
 24. Ward SJ. 1998 Numbers of teats and pre-and post-natal litter sizes in small diprotodont marsupials. *J. Mammal.* **79**, 999–1008. (doi:10.2307/1383108)
 25. Charnov EL, Schaffer WM. 1973 Life history consequences of natural selection: Cole's result revisited. *Am. Nat.* **107**, 791–793. (doi:10.1086/282877)
 26. Krajewski C, Woolley PA, Westerman M. 2000 The evolution of reproductive strategies in dasyurid marsupials: implications of molecular phylogeny. *Biol. J. Linnean Soc.* **71**, 417–435. (doi:10.1111/j.1095-8312.2000.tb01267.x)
 27. Oakwood M, Bradley AJ, Cockburn A. 2001 Semelparity in a large marsupial. *Proc. R. Soc. B* **268**, 407–411. (doi:10.1098/rspb.2000.1369)
 28. Dickman C, Braithwaite R. 1992 Postmating mortality of males in the Dasyurid Marsupials, *Dasyurus* and *Parantechinus*. *J. Mammal.* **73**, 143–147. (doi:10.2307/1381875)
 29. Jones M, Dickman CR, Archer M. 2003 *Predators with pouches: the biology of carnivorous marsupials*. Collingwood, Melbourne: CSIRO Publishing.
 30. Fisher DO, Blomberg SP. 2011 Costs of reproduction and terminal investment by females in a semelparous marsupial. *PLoS ONE* **6**, e15226. (doi:10.1371/journal.pone.0015226)
 31. Fisher DO, Nuske S, Green S, Seddon JM, McDonald B. 2011 The evolution of sociality in small, carnivorous marsupials: the lek hypothesis revisited. *Behav. Ecol. Sociobiol.* **65**, 593–605. (doi:10.1007/s00265-010-1060-7)
 32. Collett RA, Fisher DO. 2017 Time-lapse camera trapping as an alternative to pitfall trapping for estimating activity of leaf litter arthropods. *Ecol. Evol.* **7**, 7527–7533. (doi:10.1002/ece3.3275)
 33. Climate Data Online: Australian Government. 2016 [cited 2016]. See <http://www.bom.gov.au/climate/data/>.
 34. Colwell RK. 1974 Predictability, constancy, and contingency of periodic phenomena. *Ecology* **55**, 1148–1153. (doi:10.2307/1940366)
 35. Johnson C. 1998 Rarity in the tropics: latitudinal gradients in distribution and abundance in Australian mammals. *J. Anim. Ecol.* **67**, 689–698. (doi:10.1046/j.1365-2656.1998.00232.x)
 36. Paradis E, Claude J, Strimmer K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)
 37. Pinheiro J, Bates D, DebRoy S, Sarkar D. 2018 Linear and Nonlinear Mixed Effects Models.
 38. May-Collado LJ, Kilpatrick CW, Agnarsson I. 2015 Mammals from 'down under': a multi-gene species-level phylogeny of marsupial mammals (Mammalia, Metatheria). *PeerJ* **3**, e805. (doi:10.7717/peerj.805)
 39. Symonds MR, Blomberg SP. 2014 A primer on phylogenetic generalised least squares. In *Modern phylogenetic comparative methods and their application in evolutionary biology*. pp. 105–130. Berlin, Germany: Springer.
 40. Grafen A. 1989 The phylogenetic regression. *Phil. Trans. R. Soc. B* **326**, 119–157. (doi:10.1098/rstb.1989.0106)
 41. Nagelkerke NJ. 1991 A note on a general definition of the coefficient of determination. *Biometrika* **78**, 691–692. (doi:10.1093/biomet/78.3.691)
 42. Reside AE, VanDerWal J, Kutt AS. 2012 Projected changes in distributions of Australian tropical savanna birds under climate change using three dispersal scenarios. *Ecol. Evol.* **2**, 705–718. (doi:10.1002/ece3.197)
 43. Dunlop JN, Saule M. 1982 The habitat and life history of the Pilbara ningau Ningau timealeyi. *Rec. West. Aust. Mus.* **10**, 47–52.
 44. Read D. 1995 Gile's planigale. In *The Australian museum complete book of Australian mammals* (ed. R Strahan), pp. 107–109. Sydney, Australia: Reed Books.
 45. Speakman JR, Król E. 2010 The heat dissipation limit theory and evolution of life histories in endotherms—time to dispose of the disposable soma theory? *Integr. Comp. Biol.* **50**, 793–807. (doi:10.1093/icb/icc049)
 46. Selman C, Blount JD, Nussey DH, Speakman JR. 2012 Oxidative damage, ageing, and life-history evolution: where now? *Trends Ecol. Evol.* **27**, 570–577. (doi:10.1016/j.tree.2012.06.006)
 47. Kirkwood TB, Holliday R. 1979 The evolution of ageing and longevity. *Proc. R. Soc. Lond. B* **205**, 531–546. (doi:10.1098/rspb.1979.0083)
 48. Healy K *et al.* 2014 Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc. R. Soc. B* **281**, 20140298. (doi:10.1098/rspb.2014.0298)
 49. Reznick DN, Bryant MJ, Roff D, Ghalambor CK, Ghalambor DE. 2004 Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature* **431**, 1095. (doi:10.1038/nature02936)
 50. Orzack S H, Tuljapurkar S. 2001 Reproductive effort in variable environments, or environmental variation is for the birds. *Ecology* **82**, 2659–2665. (doi:10.2307/2679944)
 51. Becker FS, Tolley KA, Measey GJ, Altwegg R. 2018 Extreme climate-induced life-history plasticity in an amphibian. *Am. Nat.* **191**, 250–258. (doi:10.1086/695315)
 52. Nilsen EB, Gaillard JM, Andersen R, Odden J, Delorme D, Van Laere G, Linnell JD. 2009 A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *J. Anim. Ecol.* **78**, 585–594. (doi:10.1111/j.1365-2656.2009.01523.x)
 53. Clutton-Brock TH. 1984 Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* **123**, 212–229. (doi:10.1086/284198)
 54. Descamps S, Boutin S, McAdam AG, Berteaux D, Gaillard J-M. 2009 Survival costs of reproduction vary with age in North American red squirrels. *Proc. R. Soc. B* **276**, 1129–1135. (doi:10.1098/rspb.2008.1401)
 55. Clutton-Brock TH, Guinness FE, Albon SD. 1982 *Red deer: behavior and ecology of two sexes*. Chicago, IL: University of Chicago press.
 56. Cody ML. 1966 A general theory of clutch size. *Evolution* **20**, 174–184. (doi:10.1111/j.1558-5646.1966.tb03353.x)
 57. Williams GC. 1966 Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**, 687–690. (doi:10.1086/282461)
 58. Sibly RM, Brown JH. 2007 Effects of body size and lifestyle on evolution of mammal life histories. *Proc. Natl Acad. Sci. USA* **104**, 17 707–17 712. (doi:10.1073/pnas.0707725104)
 59. Ashmole NP. 1963 The regulation of numbers of tropical oceanic birds. *Ibis* **103**, 458–473.
 60. Badyaev AV, Ghalambor CK. 2001 Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. *Ecology* **82**, 2948–2960. (doi:10.1890/0012-9658(2001)082[2948:EOLHAE]2.0.CO;2)
 61. Bywater KA, Apollonio M, Cappai N, Stephens PA. 2010 Litter size and latitude in a large mammal: the wild boar *Sus scrofa*. *Mamm. Rev.* **40**, 212–220.
 62. Lord Jr RD. 1960 Litter size and latitude in North American mammals. *Am. Midland Nat.* **64**, 488–499. (doi:10.2307/2422677)
 63. Bunnell F, Tait D. 1981 *Population dynamics of bears—implications. Dynamics of large mammal populations*, pp. 75–98. New York, NY: John Wiley and Sons.
 64. Beckman J, Banks SC, Sunnucks P, Lill A, Taylor AC. 2007 Phylogeography and environmental correlates of a cap on reproduction: teat number in a small marsupial, *Antechinus agilis*. *Mol. Ecol.* **16**, 1069–1083. (doi:10.1111/j.1365-294X.2006.03209.x)
 65. Congdon J, Dunham A, Tinkle D. 1982 Energy budgets and life histories of reptiles. In *Biology of the Reptilia* (eds C Gans, FH Pough), pp. 233–271. New York, NY: Academic Press.
 66. Jones JH. 2011 Primates and the evolution of long, slow life histories. *Curr. Biol.* **21**, R708–RR17. (doi:10.1016/j.cub.2011.08.025)
 67. Danforth BN. 1999 Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. *Proc. R. Soc. B* **266**, 1985–1994. (doi:10.1098/rspb.1999.0876)
 68. Lovich JE, Ennen JR, Yackulic CB, Meyer-Wilkins K, Agha M, Loughran C, Bjurlin C, Austin M, Madrak S. 2015 Not putting all their eggs in one basket: bet-hedging despite extraordinary annual reproductive output of desert tortoises. *Biol. J. Linnean Soc.* **115**, 399–410. (doi:10.1111/bij.12505)

69. Stearns SC. 1976 Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51**, 3–47. (doi:10.1086/409052)
70. Gaillard J-M, Festa-Bianchet M, Yoccoz NG. 1998 Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* **13**, 58–63. (doi:10.1016/S0169-5347(97)01237-8)
71. Wilkinson GS, South JM. 2002 Life history, ecology and longevity in bats. *Aging Cell* **1**, 124–131. (doi:10.1046/j.1474-9728.2002.00020.x)
72. Reznick DA, Bryga H, Endler JA. 1990 Experimentally induced life-history evolution in a natural population. *Nature* **346**, 357. (doi:10.1038/346357a0)
73. Ghalambor CK, Martin TE. 2001 Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**, 494–497. (doi:10.1126/science.1059379)
74. Turbill C, Bieber C, Ruf T. 2011 Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proc. R. Soc. B* **278**, 3355–3363. (doi:10.1098/rspb.2011.0190)