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Environmental effects and individual body condition drive seasonal fecundity of rabbits: identifying acute and lagged processes

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Running title: Acute and lagged processes in seasonal fecundity

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Abstract

The reproduction of many species is determined by seasonally-driven resource supply. But it is difficult to quantify whether the fecundity is sensitive to short or long-term exposure to environmental conditions such as rainfall that drive resource supply. Using 25 years of data on individual fecundity of European female rabbits, *Oryctolagus cuniculus,* from semiarid Australia, we investigate the role of individual body condition, rainfall and temperature as drivers of seasonal and long-term and population-level changes in fecundity (breeding probability, ovulation rate, embryo survival). We built distributed lag models in a hierarchical Bayesian framework to account for both immediate and time-lagged effects of climate and other environmental drivers, and possible shifts in reproduction over consecutive seasons. We show that rainfall during summer, when rabbits typically breed only rarely, increased breeding probability immediately and with time lags of up to 10 weeks. However, an earlier onset of the yearly breeding period did not result in more overall reproductive output. Better body condition was associated with an earlier onset of breeding and higher embryo survival. Breeding probability in the main breeding season declined with increased breeding activity in the preceding season and only individuals in good body condition were able to breed late in the season. Higher temperatures reduce breeding success across seasons. We conclude that a better understanding of seasonal dynamics and plasticity (and their interplay) in reproduction will provide crucial insights into how lagomorphs are likely to respond and potentially adapt to the influence of future climate and other environmental change.

Keywords Invasive species, lagged effects, dynamic optimization, reproduction, seasonality

Introduction

The reproduction of many species is limited to seasonal time windows of suitable thermal conditions and sufficient food supply (Bronson 1985; Hone and Clutton-Brock 2007). As such, the magnitude and seasonal timing of changing environmental conditions can affect reproduction and population dynamics more generally.

Fecundity (the average per-capita number of offspring per breeding season) consists of a sequence of components from ovulation to recruitment of offspring into populations, each of which can be limited by food restriction and environmental stress such as unfavourable temperatures. For example, an increase in food availability can result in more females breeding (Desy and Thompson 1983) and larger litter sizes (Stockley 2003). A prolonged breeding season can allow for repeated reproduction for iteroparous mammals, leading to substantial increases in annual population growth (Swihart 1984). Food restriction and environmental stress over prolonged periods can also limit ovulation rates in mammals (Bronson 2009) and the timing of sexual receptivity, whereas immediate environmentally- or socially-driven stress during pregnancy imposes a risk on successfully carrying embryos to term (Ashworth et al. 2009).

In seasonal environments, fecundity can be affected by phenology, whereby there is a need to match resource availability (within and among seasons and years) with the timing of reproduction (Via et al. 1995). Often, reproduction among vertebrates from temperate latitudes is timed to coincide with circannual rhythms of hormonal changes, food intake, and energy expenditure (Ebling and Barrett, 2008). Species well adapted to highly fluctuating environments, can maximise their reproductive success by having extended reproductive periods to compensate for immediate resource shortage or environmental stress (Jonzén et al. 2010; Lof et al. 2012). Therefore, plasticity in species' reproductive biology and behaviour in response to changes in environmental factors (exposure-response relationship) is necessary for many species to respond to short-term environmental fluctuations (Meyers and Bull 2002), and potentially long-term shifts in environmental resources.

Quantifying the relevant timespan of the exposure to environmental stress, in addition to the overall strength of environmental drivers, can provide important insights into the resilience of reproduction to climate and other environmental change (Sæther et al. 2000; Thompson and Ollason 2001). Measuring reproductive responses to environmental fluctuations requires teasing apart seasonal and long-term trends, which, in some cases, can be driven by similar climate (and other environmental) drivers. For example, if a late onset of seasonal food availability results in less overall annual breeding because of a short breeding season, variation in seasonal and inter-annual breeding patterns are tightly linked to each other. In contrast, if the seasonal onset of breeding does not affect the overall (population-level) annual reproductive output, environmental drivers of seasonal and long-term reproductive trends are not necessarily the same (Fig. 1). Because seasonal variation in reproductive output can affect inter-annual population abundance it is important to understand how environmental drivers can affect reproductive performance across season, particularly for species of management concern, such as pest or threatened species. Progress towards understanding how individual traits (e.g., body condition) and climate (e.g., variation in temperature and rainfall) and other environmental conditions (e.g., pasture growth) affect reproduction and early survival is mostly limited to large mammals based on longitudinal recapture studies of individuals marked at birth (e.g. Plard et al. 2015). These effects are not as well understood in small mammals, where data on critical stages of their life cycles is often missing (Aars and Ims 2002; Lambin and Yoccoz 2001); and population dynamics of mammals with high fecundity rates and cyclic dynamics (e.g. voles, lemmings) are often believed to be driven by variation in predation rates (e.g. Hanski et al. 2001).

Here we examine the long-term effects of climate and other environmental drivers (e.g., soil moisture and pasture biomass) and individual body condition on the fecundity of European rabbits, *Oryctolagus cuniculus*, a polytocous and iteroparous mammal. Rabbits have considerable reproductive plasticity, being able to repeatedly reproduce within a single breeding season with varying litter sizes (Brambell 1942). Rabbit reproduction in Australia is tightly linked to seasonally limited food availability, and more specifically the weather conditions that promote plant growth (Myers 1970). Females can become pregnant within 10 days of rains that produce germination and sprouting of grasses and herbs (Myers 1970). Plasticity in the timing of reproduction (i.e. the probability a female reproduces at a certain time) and ovulation rate (i.e. the investment in a certain number of embryos) is likely to cause an observed geographic gradient in the timing of peak pregnancy and ovulation rates across Australia (Gilbert et al. 1987). Furthermore, rabbits can resorb embryos during pregnancy and this is likely to occur during stressful conditions (Brambell 1942; Conaway et al. 1960). The sensitivity of long-term changes in the timing and success of reproduction (i.e., probability of being pregnant, ovulation rate and embryo survival) to temporal variation in environmental conditions has, until now, not been explored for any lagomorph species.

We employ a novel multifaceted approach, which accounts for the effect of immediate and lagged environmental conditions, to disentangle the drivers of individual- and group-level changes in rabbit fecundity rates. Often there is no *a priori* knowledge about the time period of exposure that is likely to influence changes in any of the various components of fecundity (i.e., probability of being pregnant, ovulation rate and embryo survival). Distributed lag models (DLM) can help overcome this problem, by avoiding aggregating and averaging covariates over arbitrary periods (Almon 1965; Gasparrini et al. 2010; Schwartz 2000). Here we incorporate distributed lag models into a Bayesian multilevel model framework to investigate the relative importance of individual and environmental condition on seasonal and long-term changes in rabbit fecundity. We use this novel statistical approach to identify the mechanisms and time scales by which environmental conditions affect rabbit fecundity. Distributed time lag models have previously been applied in medical sciences (Schwartz 2000), but their benefit has to date not been tested in ecology.

Materials and methods

Study area

Our study site was located at Belton (-32.224S 138.708E) in the Flinders Range, South Australia. The study site is at the southern limit of a semi-arid climate zone and is characterised by cool winters and warm and dry summers. Pastures at Belton consist of a mixture of native and introduced grasses and forbs (*Stipa* spp., *Hordeum* spp., *Bromus* spp., *Echium plantagineum, Medicago* spp.), including arid-zone species (*Atriplex* spp., *Sclerolaena* spp.) on shallow, loamy soils (Cooke 2014). Pasture growth is seasonal, with a decreasing herbaceous biomass during summers. Temperatures above 35 °C often occur for more than five consecutive days in summer causing considerable stress on herbaceous plants (Cooke 2014). The largely nocturnal behaviour of rabbits helps them avoid temperature extremes, because the ambient temperature in rabbit burrows is fairly constant diurnally, exhibiting only minor variation over seasons (Cooke 1990).

Demographic and environmental data

Necropsy data

Our data set consisted of 2,563 females shot between 1968 and 1993 during 199 field surveys. Approximately 30 rabbits were shot by authorized shooters at approximately six week intervals and reproductive status recorded after dissection. All applicable institutional and/or national guidelines for the care and use of animals were followed. Rabbits were shot in the order they were encountered. There is a size bias in the sampling technique with young individuals (< 1000 g for rabbits) being underrepresented in samples of visual encounter. There was no indication that gestating females were more likely to be shot than non-gestating females.

Body mass was recorded to the nearest ± 25 g for entire and eviscerated bodies (removing all intestinal and urogenital organs), using a Salter dial spring balance. We used the latter measure in our study to exclude any bias in body mass due to reproduction. Animals were sexed and ovaries of females were examined for follicles and *corpora lutea* and their number recorded. For each uterine horn we recorded the number of embryos. Embryos of < 7 days gestation cannot be counted as they have not been implanted, but pregnancy can be recognised because of vascular uterine tissues and recent follicles on the ovaries. Stage of gestation for embryos > 7 days old was classified according to the shape and size of embryos (Minot and Taylor 1905), allowing for shorter gestation in wild rabbits, i.e. 28 days at our study site (Cooke 1974).

We used the dry weight of fixed eye lenses as a surrogate for individual age. This is possible because eye lenses grow continuously through life independent of nutritional conditions (Dudzinski and Mykytowycz 1961). We did not directly transform eye lens weight into an age estimate because this is inaccurate for fully-grown rabbits − an artefact of the underlying logistic growth relationship (Dudzinski and Mykytowycz 1961). Fat coverage of the kidneys was scored between 0-5 based on a visual assessment of the peri-renal fat visible (0: no fat, 5: kidney completely covered in fat). Kidney fat scores provide good indication of short-term nutritional condition (Henke and Demarais 1990); for simplicity, we treated this ordinal variable as a continuous covariate in our analysis.

We predicted the (average) weight for rabbits of all ages by fitting a growth function (West et al. 2001) to all measures of body mass in relation to eye lens weight (a proxy of age). We then calculated a body mass index for all individual using the difference between observed and predicted body mass (the residuals). Large positive values indicated observed body masses above average weight-for-age and vice versa i.e., negative values indicate less weight than average (see electronic supplementary material ESM 1).

Abundance surveys

Rabbit relative abundance counts were conducted at Belton between 1965 and 1994 prior to necropsy surveys. Rabbits were counted from a vehicle driven at constant speed (8 km/h) along an 8-km-transect using quartzhalogen spotlight (100 W, ca. 80 m beam range) (Cooke 1983). Counting was repeated between 2-6 times on consecutive nights. During the 30-year study period, the rabbit population at Belton experienced human management, directly affecting the population abundance. In particular, the European Rabbit Flea, *Spilopsyllus cuniculi*, was released at a nearby field site in 1969, causing the spread of myxomatosis and a considerable decline in the rabbit population (Cooke 1983) (electronic supplementary material ESM 1, Fig. E.1.3).

Climate and environmental data

We generated average daily measures of maximum temperature and rainfall per week for Belton using the daily records from the SILO, Australian climate database (Jeffrey et al. 2001). We calculated a soil moisture index by adding the rainfall for each day and subtracting 0.2 times the evaporation from a free-water surface from the previous day. We imposed a maximum value of 100 to account for soil saturation. A similar approach was found to do a good job at approximating major changes in soil moisture conditions at a closely located site (Cooke unpublished data). From this time series, we also generated weekly average measures of weather for our analysis. We estimated monthly growth of total standing dry matter of herbaceous plants (difference in pasture biomass kg/ha), using output from the *AussieGrass* model (Carter et al. 2000). We used this as a proxy for food availability (Roxburgh et al. 2004).

Statistical analysis

We used generalized linear models, fitted in a Bayesian framework, to examine the potential drivers of variation in breeding probability (the probability of being pregnant), ovulation rate and embryo survival. We assumed that the recorded instance $z(i,t)$ that female i is pregnant at survey time t follows a Bernoulli distribution given the breeding probability $\varphi(i,t)$, which we linked to covariates with a logit link function. Given that reproduction of rabbits is highly seasonal, we allowed all dependent parameters to vary across season s classified as 1) January – April (rare breeding in summer due to dry weather and shortage in food supply), 2) May-June (early breeding after the onset of pasture growth), 3) July – October (main breeding period), and 4) November – December (late breeding). The model for breeding probability can be described as:

Breeding probability ~ day of year + Eye lens weight + individual body condition + environmental data over time lags + density dependence + breeding probability at preceding time step (group-level).

This can be expressed mathematically as:

$$z(i,t) \sim Bernoulli[\varphi(i,t)] \qquad \text{(eqn 1)}$$

and

$$\mathrm{logit}[\varphi(i,t)] \sim \beta^{\varphi}{}_{0}(y) + X_{Jlday}(i)B^{\varphi}{}_{Jlday}(s) + X_{Age}(i)B^{\varphi}{}_{Age}(s) + X_{Ind}(i)B^{\varphi}{}_{Ind}(s) +$$

$$X_{Env}(t,..L_{Env})\Theta^{\varphi}{}_{Env}(s) + \Theta_{N}{}^{\varphi}(s)N(t,..L_{N})) + \beta^{\varphi}{}_{Prev}(s)\ \mu_{\varphi}(t-1)) \qquad \text{(eqn 2)}$$

where X_{Jlday} and X_{Age} are matrices of Julian day of capture and individual age of 4th orthogonal polynomial order, respectively; X_{Ind} is a matrix of individual body condition covariates; $B^{\varphi}(s)$ are season-specific coefficient estimates for these covariates. Note that the superscript '$^{\varphi}$' is used as we implemented the same model equations for modelling variation in ovulation rate and embryo survival. X_{Env} and N comprise arrays of environmental covariates and population size respectively, with values from consecutive time steps measured between time t and the maximum time lag L_{Env} and L_N, respectively.

We used distributed lag models (DLM) (Welty et al. 2009) to avoid aggregating covariates over an arbitrary number of time steps. The DLM regresses the response variable against the lagged covariates (i.e. for time t against covariates at times $t-1$, $t-2$ etc.). Our model assumes that the effects of the covariates up to lag time π are of similar magnitude (i.e. assuming a multivariate prior distribution), after which they shrink towards zero. We estimated the parameter π for each DLM. We considered the average of the vector Θ notated as $\hat{\theta}$ as overall effect size from DLMs (see electronic supplementary material ESM 2).

To address the effect that breeding activity is likely biased by earlier attempts, we included a 1st order auto-regression term μ_{φ} of the average breeding probability in the preceding seasonal time step in the model. It is unlikely that the removal of individuals would bias average breeding probability because the number of females removed was very low and population size large. To do this, we modelled μ_{φ} as the average breeding probability in each year y and season s, assuming that coefficient estimates for β^{φ}_{Prev} indicate shifting breeding probability over consecutive time steps/ seasons.

We modelled ovulation rates (individual counts of *corpora lutea*), $w(i,t)$, using a mixed log-normal-Poisson likelihood. We then modelled the log-scale mean of counts $\mu_w(i,t)$ using the same covariates as given in equation 1.

We modelled embryo survival rates (i.e. the proportion/number of ova that resulted in embryos to 28 days $y(i,t)$ carried) as a fraction of $w(i,t)$ using a binomial distribution. This is because for each ova in $w(i,t)$, there is a success rate $\rho(i,t)$ that it will result in a fully developed embryo after 28 days. Thus, we assumed

$$y(i,t) \sim Bin[w(i,t), \rho(i,t)^{\delta(i)}] \quad \text{(eqn 3).}$$

We used the exponential scaling factor $\delta(i)$ to correct for observation bias in $\rho(i,t)$, which we calculated as the time during the gestation period when embryos were counted (embryo age at dissection time) divided by the total length of the gestation period (28 days). In a preliminary analysis we found evidence that embryos are progressively resorbed during gestation (**Appendix S.1.3**). The logit link function was then used to model variation in $\rho(i,t)$ in response to covariates as given in equation 1.

We used an open population model with a mixed binomial-Poisson likelihood (Aubry et al. 2012; Royle 2004; Zellweger-Fischer et al. 2011) to estimate rabbit relative abundance for each time step, v, during the population survey and then assigned values to $N(t)$ (relative abundance) based on time differences of no more than 10 days between t and v (i.e. necropsy and spotlight count data). To do this, we modelled counts $c(v,k)$ for the repeated surveys during time step v as:

$$c(v,k) \sim Bin[N(v), p(k)] \text{ and } N(v) \sim Pois[\omega(y,m)]$$

where detection probability $p(k)$ was allowed to vary over months and in response to maximum temperature and rainfall during the day of survey. Abundance indices $N(v)$ were assumed to be random draws from the density $\omega(y,m)$, varying over years y and months m. See electronic supplementary material ESM 2 for details of the model code and ESM 1 Fig. S.1.1 for estimated abundance indices.

We used the freeware JAGS 3.4.0 for sampling and model fitting, operated via the R statistical platform with the package *rjags* (Plummer 2003). We used Markov Chain Monte

Carlo (MCMC) sampling in a Bayesian framework to select the polynomial order for the age-related regression terms with equal priors for each order. We used a Gibbs variable selection (GVS) procedure for joint sampling of the most likely polynomial order and coefficient values (Dellaportas et al. 2002; O'Hara and Sillanpää 2009). The posterior selection frequency *ι(v)* indicated the relative importance of selected variables *v*, while the use of pseudo-priors ensured accurate coefficient estimates (Wells et al. 2014). Likewise, we used GVS to select all other variables (except those with time lags) in the model; we do this because seasonally variable coefficient estimates led to a large parameter space. All covariates were scaled (centred values divided by one SD).

We applied posterior predictive model diagnostics to assess whether the model assumptions are good approximations of the data generating process. Bayesian p-values around 0.5 indicate good fit whereas values close to 0 or 1 indicate an increasing discrepancy between model predictions and observation data (Gelman et al. 1996). We also calculated Bayesian p-values for models where we replaced all DLMs with models for single covariates calculated as either immediate measures (environmental conditions measured during the same week as the response variable) or those measured at an arbitrary 10 week period prior to when the response variables was measured. This allowed us to directly test whether DLMs provided a better fit or not to the observation data.

We show all estimates as posterior modes and 95 % highest posterior credible intervals (CI). CIs that did not include zero were considered ‘significant’. All posterior coefficient estimates, frequencies of variable selections and summary statistics for covariates are provided in **ESM 2**.

Results

Breeding probability

The breeding probability of rabbits was highly seasonal, with low probabilities in January – April (summer breeding season, a period when rabbits reproduce infrequently), increasing in May-June (early breeding season), peaking in July – October (main breeding season), before declining in November – December (late breeding season) (Fig. 2). The distribution of breeding probabilities within years (and seasons) differed markedly across years as did the overall yearly breeding probabilities (Fig. 2). In many years, the annual polynomial fit of breeding probability matched field observations. For example breeding activity was delayed and reduced in very dry years (e.g. 1972, 1982) and increased over prolonged breeding seasons in wet years (e.g.1973, 1974) (Fig. 2).

We found support for a strong effect of rainfall on breeding probability, but only during the summer breeding season, where breeding probability was 22 % higher for each additional mm of rainfall (odds ratio of 1.2, CI: 1.1 – 1.4, i.e. from 0.17 to 0.21 breeding probability in summer). Note that 1-10 mm rain per week typically represents heavy summer rain, as most days are rainless (ESM 1, Fig. E.1.2). Distributed lag models showed that rainfall affects breeding probability in the summer breeding season immediately and up to time lags of 10 weeks (CI: 5-20) (Fig. 3) This indicates that in years with good rainfall, the onset of breeding activity is much earlier. We detected an effect of temperature on breeding probability in all seasons except the late breeding season, with decreases in breeding probability between 3.7 – 4.6 % (odds ratios 0.7 – 0.9 all CIs: 0.6 – 0.9 %) per °C increase in temperature. Temperature effects were both immediate and with time lags of up to 10 weeks (CI: 0-15) in the early breeding season. The temporal distribution of time lagged effects for temperature in the other two seasons were inconclusive.

Breeding probability was influenced by kidney fat scores in the summer breeding season, whereby breeding probability increased 146 % (odds ratio 3.9, CI: 2.5 – 6.1) for every unit of increase in kidney fat score (ordinal scores between 0 and 5). Individual body mass index had a positive impact on breeding probability in the main and late breeding season, with an increase of breeding probability between 0.4 and 1.7 % (odds ratios 3.4 – 5.0 all CIs: 1.9 – 9.0 %) per unit increase in body mass index (i.e. g above expected average body mass). This suggests that kidney fat scores can affect the start of the breeding season (whereby high scores promote an earlier onset of breeding), while body mass index affects breeding probability only towards the end of the annual breeding cycle (Fig. 4).

Breeding probability decreased significantly during the main breeding season if breeding probability was high in the preceding (early breeding) season (Appendix A2), suggesting that shifts towards earlier reproductive output can result in the exhaustion of breeding potential later in the annual cycle. Breeding probability increased with age (eye lens weight) of individuals. Furthermore, young individuals with lens weights between 150 and 200 mg (corresponding to 130 to 230 days old individuals) were more likely to breed in the later part (July – Dec) of the annual breeding cycle (ESM 1, Fig. E.1.5). This suggests that rabbits born early in the year were likely to breed later during the year, leading to relatively more young rabbits breeding in the later part of the annual cycle.

We found no evidence for any direct effects of population density, soil moisture or pasture growth indices on breeding probability (i.e. all CI indistinct from zero). Model fit was good with a Bayesian p-value of 0.42, suggesting that the covariates did a reasonably good job at describing variation in the data. When using single-step covariates instead of distributed lag models, the Bayesian p-values were 0.86 and 0.93 for immediate and 10-week lagged effects, respectively. This shows that the use of distributed lag models improved model fit to the observation data for breeding probability.

Ovulation rate

The overall average ovulation rate was 6 *corpora lutea* (SD 1.7). Ovulation rate was almost constant across the breeding season in some years, but exhibited (a-seasonal) variation in others (ESM 1, Fig. E.1.3). We found an effect of rainfall on ovulation rate during the main breeding season, whereby ovulation rate increased by 0.01 *corpora lutea* above average (log-normal coefficient 0.006 CI: 0.001 – 0.015) per 1 mm increase in rainfall. Our model showed greatest support for a rainfall effect with time lags of up to 14 (CI: 1 - 19) weeks. Ovulation rates were also influenced by body mass index. Body mass index had a positive effect on ovulation rate during the early to late breeding season with 0.12 – 0.19 increases in ovulation rate per unit change in body mass index (all CIs: 0.04 – 0.25). The model fit was reasonably good with a Bayesian p-value of 0.56. When using single-step covariates instead of distributed lag models, the Bayesian p-values were 0.55 and 0.56 for immediate and 10-week lagged effects. This means that the distributed lag model did not improve fit to the observed data for ovulation rates.

Embryo survival rates

The overall estimated embryo survival rate was around 72 % (CI: 71 – 74 %). Embryo survival rates exhibited variation in some years (see ESM 1, Fig. E.1.4). We show that kidney fat score had a positive impact on embryo survival only during the rare breeding season, with an increase of 109 % (odds ratio 2.9 CI: 1.8 – 5.8 %) in survival rate per unit increase in kidney fat score. Likewise, body mass index is likely to influence embryo survival rates, particularly during the summer breeding season, where survival increased by 0.7 % (odds ratio 3.9 CI: 2.1 – 8.8 %) per g above average body mass. However, overall model fit for embryo survival was poor with a Bayesian p-value of zero, meaning that the covariates had a low predictive power in explaining variation in embryo survival.

Discussion

Rabbits can exhibit highly seasonal and circannual patterns in their reproduction, synchronising paternal investment with food availability (Gilbert et al. 1987). We show that the effects of environmental drivers and individual body condition on long-term changes in rabbit fecundity vary considerably across seasons. Variation in rabbit fecundity was more strongly correlated to variation in individual body condition than direct changes in environmental factors. Rabbit body condition varied considerably among individuals captured at the same time, leading to high levels of individual heterogeneity in reproductive output and in embryo survival. Shifts in reproductive outputs across consecutive seasons in response to individual trait variation and, to a lesser extent, environmental conditions, are therefore likely to mitigate future climate shifts from having a direct or indirect (through body condition) effect on annual fecundity.

The effects of individual body condition and environmental factors on rabbit fecundity found in our study provide not only crucial insights into how average fecundity rates may change over time, but also how the dynamics of reproductive output are likely to shift across season. We show that variations in the timing of reproductive output are driven by the yearly onset of rainfall, potentially being mediated through food availability (Myers 1970). The lack of any direct effect of the pasture growth index on fecundity in our analysis could be due to at least two possible explanations: true pasture growth is poorly represented by our index, which unlike rainfall is not measured directly; or, total pasture growth is not representative of the local plant species consumed by rabbits. Rainfall and kidney fat score had a positive effect on breeding probability and embryo survival early in the year (January - April), suggesting that fat reserves promote reproductive success particularly when conditions are marginal (i.e. at the onset of plant growth or at the end of the breeding season when food resource become scarce)(Mutze 2009).

By using distributed lag models, we were able to show that rainfall affects breeding immediately and also with a time lag of up to ten weeks after the onset of rainfall in summer. There was, however, noticeable uncertainty in the coefficient estimates for the distributed lag models as shown by relatively large credible intervals (see Fig. 3). In very dry years, rabbits at our study site did not start breeding until mid-winter when evaporation is sufficiently low that even small amounts of rain may initiate some pasture growth (personal observation, B.C.). Such shifts in the onset of breeding may allow rabbits to minimise the effects of short-term adverse environmental conditions. Mature females that lack sufficient food resources to reproduce early in the breeding season may still be able to increase individual body condition and thereby increase their chances of later successful reproduction (Albon et al. 1983). A similar observation was made in Europe, where breeding by female rabbits is delayed after harsh winter conditions (Rödel et al. 2005).

The effects of both body mass index and kidney fat on embryo survival appeared to be strongest in the summer breeding season, whereas the effect of body mass index on breeding probability was not as apparent in summer (but the relevant credible intervals exhibited some overlap, see Fig. 4). We also show that rabbits shift reproductive output across consecutive seasons in response to the yearly onset of rain. Typically, only relatively heavy summer rains promote the onset of rabbit breeding, probably through initiating plant growth. Breeding probability in the main breeding season (e.g. July - October) decreased with higher breeding probability in the preceding season (May-June) of the same year. At the same time, an increase in breeding probability with better body conditions (larger body mass indices) in both the main and late breeding season (July - December) indicates that late breeders are mostly those in good body condition. Therefore body condition is likely to influence the number of litters raised per year.

Individuals in better body condition had higher ovulation rates throughout the primary breeding season (May- December), but not earlier in the year, when conditions are suboptimal for breeding. This suggests that individuals only invest in reproduction under reasonably good conditions. Shifts towards earlier breeding within a yearly cycle can lead to relatively less reproductive output later in the yearly cycle for iteroparous rabbits. This is likely to be brought about through ‘physiological exhaustion’ of individuals, who become incapable of breeding additional times within a yearly cycle (Myers and Poole 1963). The net effect of ‘physiological exhaustion’ on annual offspring production is that an earlier onset of the breeding seasons does not necessarily increase overall yearly breeding capacity unless resource supply persists for a sufficiently long period of time to promote the repeated breeding of individuals within the same year. Nevertheless, early breeding within a circannual cycle may still favour population growth because early-born rabbits generally have higher survival probabilities than those born shortly before the onset of summer (Mutze et al. 2002). For females of other relatively short-lived species, survival may reflect, to some extent, a cost of reproduction (Hamel et al. 2010).

We found only minor to moderate decreases of breeding probability with increases in temperature during most of the year. Breeding probability decreased only 3 – 5 % per 1 °C increase in temperature. This small temperature driven effect is unlikely to influence long-term population growth because reproductive output is generally high and with an average ovulation rate of six *corpora lutea* (see results), many more infants are born than can be recruited into the populations. Strong density-dependent compensation in rabbits through survival (Fordham et al. 2012b) means that minor declines in reproductive output should not alter population-level growth rates (Kokko and Lindström 1998).

The climate in semiarid Australia is predicted to experience increasing temperatures and declining rainfall in late autumn and early winter (CSIRO and Bureau of Meterology 2014). This is likely to cause increased physiological stress for rabbits (Fordham et al. 2012a). However, given that shifting reproductive output over time can to some extent compensate for adverse environmental conditions, and because overall temperature effects are not very strong, we conclude that significant reduction in reproductive output of rabbits under more extreme future climate conditions are unlikely or at least difficult to predict. In any case, our results support previous suggestions that environmentally-forced large-scale population changes are unlikely to be driven by fecundity alone, particularly for mammals with high reproductive potential (Jonzén et al. 2010; Korpimäki et al. 2004). Accordingly, studies of rabbits at another study site (Turretfield Research Station, ca. 200 km south, Mediterranean climate) show that survival rates of rabbits are controlled by weather conditions and rabbit haemorrhagic disease (which was not present in Australia during the time of our field work)(Fordham et al. 2012b; Mutze et al. 2014). Here, disease effects are tightly linked to the seasonal matching of host and pathogen dynamics (Wells et al. 2015).

We were unable to identify and model the underpinning natural processes that cause individual heterogeneity, inter-annual variability or seasonal variability in body condition. This is pertinent given that body condition is the most important driver of rabbit fecundity. Better body condition is commonly linked to food availability in rabbits (Mutze 2009), however, individual heterogeneity in rabbit body condition was not influenced by population-level processes such as density dependence, for which we would have expected a strong effect if increases in population density would equally induce stress for all individuals of a population such as food shortage. This is because high population densities would be expected to induce stress at the individual-level through food shortages. Other potential drivers of individual heterogeneity in body condition include social structure, where dominant females have better access to food and shelter (von Holst et al. 2002), and parasites (Newey and Thirgood 2004). Since rabbits are iteropoarous and exhibit overlapping breeding generations, cohort-specific dynamics and responses to environmental conditions offer another explanation for the large individual heterogeneity underpinning reproductive output (Coulson et al. 2001; Lindström and Kokko 2002).

Our dynamic statistical approach reveals the role of seasonal and long-term environmental processes on animal demography and abundance over time. A robust understanding of these processes is needed to identify long-term (inter-annual) changes in response to environmental fluctuations beyond seasonal patterns (Benton et al. 2006; Etterson et al. 2011; Wells et al. 2013). We show that modelling ecological data with strong seasonal components can require accounting for dynamic changes in species behaviour and the history of the exposure process to environmental conditions. The majority of ecological studies to date have considered only single measures or moving averages as environmental covariates in linear models (Bolker et al. 2009). However, choosing the spatiotemporal scale over which to summarize environmental covariates is often a challenging task.

In our study, we applied distributed lag models (Welty et al. 2009) in an ecologically-based context to determine the time scale at which environmental covariates are most influential on outcome variables. Distributed lag models not only provide insights into the overall strength of environmental drivers (i.e. the effect size of coefficient estimates) but also insights into the timespan of the exposure process, requiring functional constraints for dealing with the high correlation of climate and other environmental variables from consecutive time steps. In our study, the credible intervals for the possible time lags were fairly wide. Although we could have improved this by constraining priors in the model specification, we preferred not to do this for two reasons: 1) in the absence of relevant prior knowledge, more strict constraints would limit posterior distributions, and 2) by including a random estimate of the first time lag after which weights (i.e. the relative effect sizes of each measure of time lagged covariate) effectively decrease, we use a more flexible and general distributed lag model (at the cost of large posterior ranges given the uncertainty in estimates from the data). Welty et al. (2009), for example, did use a more constrained model by assuming that the strongest effect across the lagged time steps occurs always as an immediate effect, but this is unlikely to be appropriate for our system. Therefore, we recommend that future research on the use of distributed lag models in ecology should test various forms of such models that trade-off constraints and number of parameters versus flexibility in estimating the shape of exposure-response relationships.

In summary, we show that seasonal dynamics and plasticity in reproduction are crucial components for understanding long-term changes in fecundity in response to past and future environmental conditions. Examining plasticity and time-scales of demographic exposure-response relationships in reproduction under seasonal conditions for a large range of species is likely to provide important insights into how species with different life histories are capable of dealing with global change.

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Table 1. Primary climatic and individual-level drivers of rabbit fecundity (breeding probability, ovulation rate, embryo survival) according to season. Positive effects are indicated with "(+)" and negative effects with "(-)". Different colours show a gradient from low to high (yellow to red) in the magnitude of seasonal change for breeding probability, ovulation rate, embryo survival based on model results. See Methods and Results for further details.

	Jan-Apr (summer)	**May-Jun (early)**	**July-Oct (main)**	**Nov-Dec (late)**
Breeding probability	Rainfall (+)			
	Temperature (-)	Temperature (-)	Temperature (-)	
	Kidney fat score (+)		Body mass index (+)	Body mass index (+)
			Preceding breeding probability (-)	
	Age (+)	Age (+)	Age (+)	Age (+)
Ovulation rate			Rainfall (+)	
		Body mass index (+)	Body mass index (+)	Body mass index (+)
Embryo survival	Kidney fat score (+)			
	Body mass index (+)			

Fig. 1. Illustration showing possible seasonal and inter-annual differences in rabbit fecundity. The black line illustrates a three yearly cycle of breeding probabilities (i.e., probability density function for individuals breeding). In semi-arid Australia, breeding typically starts with the onset of pasture growth in autumn (early “E” breeding season) and peaks in the main breeding season (“M”) in winter. Boxes are drawn to represent consecutive seasons, whereby orange hatching shows “E” and red hatching shows “M”. The height of the boxes represents the range of breeding probabilities within these time periods. Grey arrows illustrate potential autoregression effects (i.e. the possible effect of preceding breeding probabilities on those in the current time steps). Red dots represent seasonally averaged fecundity rates for each year. The second peak in potential breeding probability occurs relatively late in the yearly cycle, causing lower fecundity rates in the early season, whereby fecundity rates in the main seasons M-1 to M-3 are similar (red dashed lines).

Fig. 2. Seasonal patterns of breeding probability for rabbits over 25 years (1968 to 1992). Black lines show the posterior mode estimates from a 4th order polynomial model, applied on an annual time step (fitted without environmental or individual-level covariates). Grey lines show underlying uncertainty in the estimates, plotted as 1,000 posterior samples.

Fig. 3. The effects of weekly averaged rainfall on rabbit breeding probability in the summer (rare) breeding season and temperature in the early breeding season. Left panels show the posterior coefficient estimates for each weekly time lag (0 – 19 weeks), vertical black bars represent 95 % credible intervals. Red lines show the posterior mode of the parameter π,

which describes the maximum time lag for which all previous lags are equally weighted in the distributed lag model (see Methods). The posterior frequency distribution of π is shown in the right panel.

Fig. 4. Effect of kidney fat and body mass score on breeding probability, ovulation rate and embryo survival in different seasons (*summer* breeding season Jan - Apr, *early* breeding May-June, *main* breeding July - Oct, and *late* breeding season Nov - Dec). Effect sizes are given as posterior modes (black squares) and 95 % credible intervals (black lines) from scaled covariates. Numbers to the right of the coefficient estimates denote importance weights for parameters based on a Gibbs variable selection procedure (see Methods).

Fig. 1

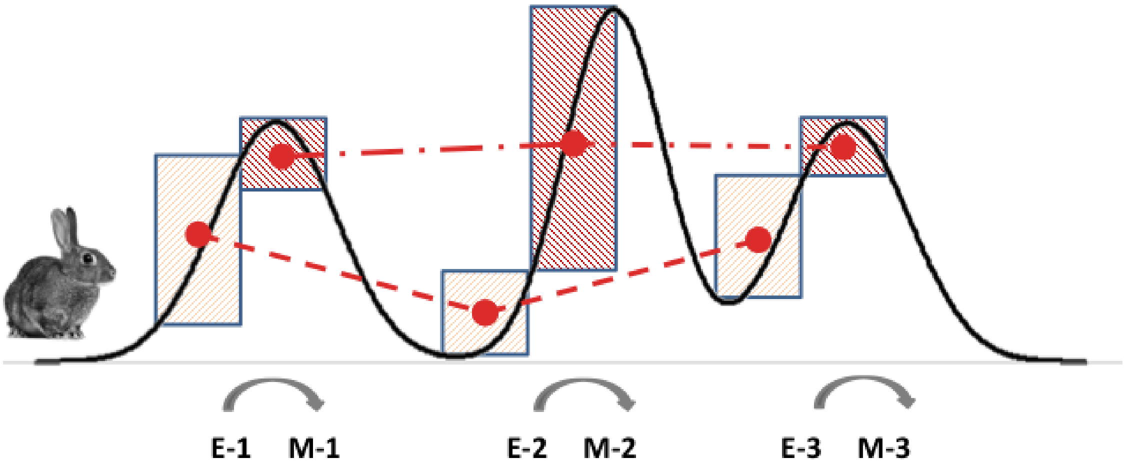
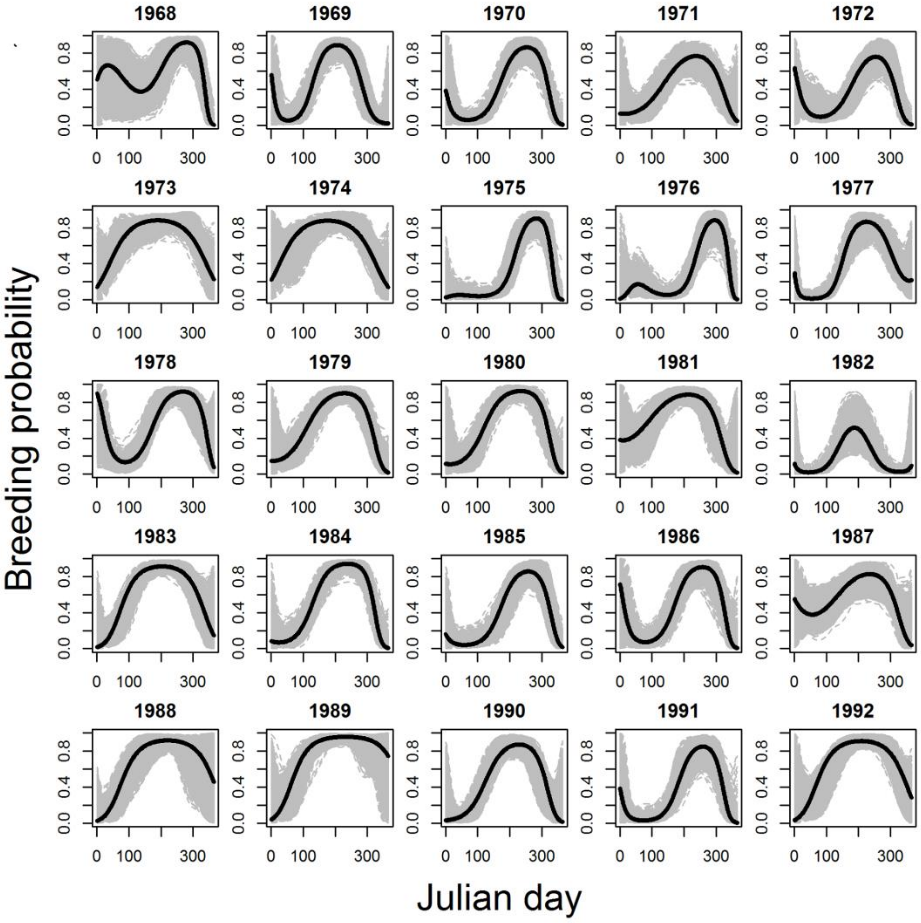


Fig. 2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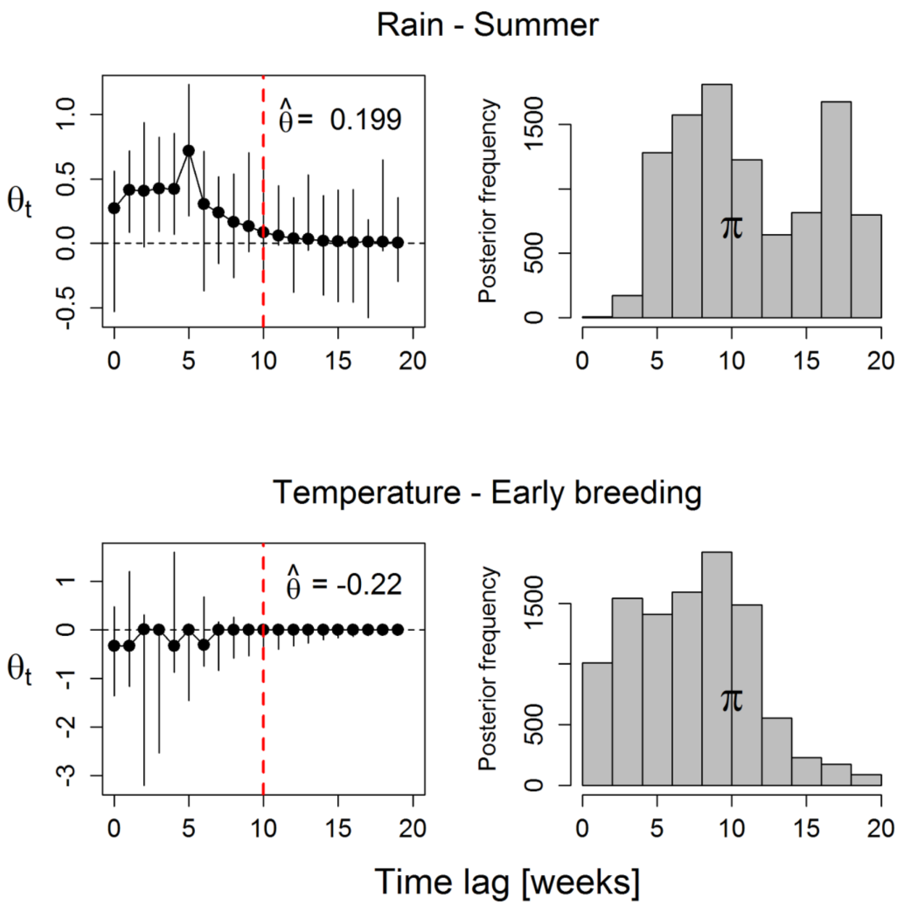
Breeding probability
Julian day

Fig. 3


Rain - Summer
θ_t
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0.0
0.5
1.0
$\hat{\theta}$= 0.199
0
5
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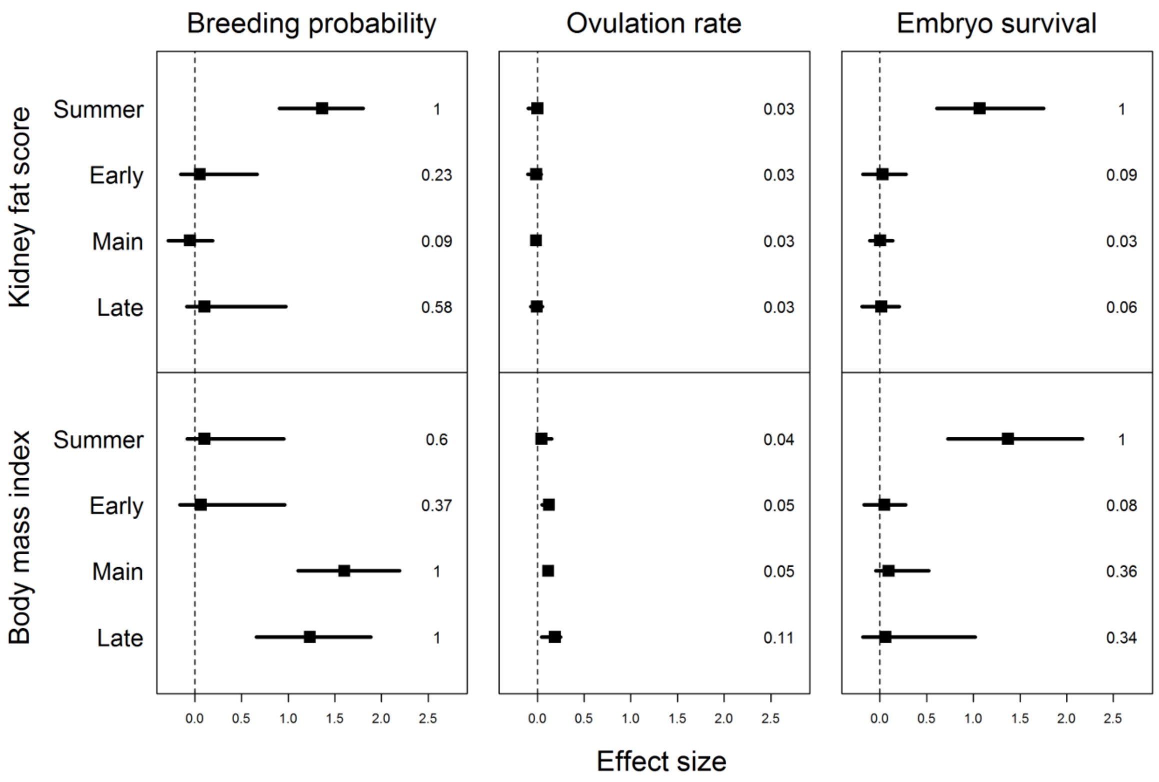
15
20
Posterior frequency
0
500
1500
π
0
5
10
15
20
Temperature - Early breeding
θ_t
-3
-2
-1
0
1
$\hat{\theta}$ = -0.22
0
5
10
15
20
Posterior frequency
0
500
1500
π
0
5
10
15
20
Time lag [weeks]

Fig. 4


Breeding probability
Ovulation rate
Embryo survival
Kidney fat score
Body mass index
Summer
Early
Main
Late
Summer
Early
Main
Late
1
0.23
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0.58
0.6
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0.05
0.11
1
0.09
0.03
0.06
1
0.08
0.36
0.34
0.0
0.5
1.0
1.5
2.0
2.5
Effect size