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Generation cycles in Indonesian lady beetle populations may occur as a result of cannibalism

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Generation cycles, population cycles with a period of approximately one generation, have been observed in a variety of field and laboratory studies. Such dynamics are predicted to arise through the effects of resource competition and cannibalism or involve consumer–natural enemy interactions. We first show, using a new highly simplified model, that generation cycles are a very common outcome of strongly age-structured intraspecific interactions involving cannibalism. We then analyse a series of unique long-term time-series of ladybeetle (Coccinellidae) abundances from tropical Indonesia. Some of the time-series display clear generation cycles, and we argue that there is strong evidence that these are caused by intraspecific cannibalism.

Keywords: age structure; cannibalism;
phytophagous insects; population dynamics; time-series

1. INTRODUCTION

Ecologists have been fascinated by population cycles since the very beginning of the subject (Elton 1924). Cyclic dynamics may be driven by regular fluctuations in the environment, but also by inter- and intraspecific interactions such as competition, predation and parasitism. Analysis of cycles has proved particularly significant in ecology as the study of their period, amplitude and regularity can be informative in understanding the biotic and abiotic causes of population change (e.g. Turchin 2002).

Classical predator–prey cycles of the type first studied by Elton (1924) typically have periods of three, four or more prey generations. Shorter cycles, with a period of approximately one generation, trivially occur in organisms with seasonally synchronized life cycles, such as many species of annual plant or temperate invertebrate, but also occur in species that can reproduce continuously throughout the year. Such dynamic patterns are called generation cycles (Gurney & Nisbet 1985; Knell 1998), and ecologists have suggested at least two different mechanisms that might be responsible for them; both mechanisms involve highly age-specific interactions.

The first mechanism involves resource competition and cannibalism. Cultures of flour beetles (*Tribolium*) show generation cycles in the densities of juvenile but not adult life-history stages. Experimental and theoretical analyses suggest that under resource limitation this is caused by cannibalism of eggs by late-instar larvae (Hastings 1987; Hastings & Costantino 1987, 1991). When larvae are abundant, they consume a majority of eggs and so inhibit recruitment to the larval stage; this results, after a time-lag, in a decrease in the frequency of cannibalism. The eggs that survive go on to produce the next cohort of cannibalistic larvae, and the result is cycles in the abundance of the juvenile stages with a period approximately equal to the oviposition-to-adult developmental lag. The lifespan of adults is longer than the developmental lag, and their abundance is relatively constant and not influenced by the pulses in maturation.

The second type of mechanism involves consumer–natural enemy interactions rather than intraspecific competition. If parasitoids or pathogens attack restricted age classes of their host, and have development times that are approximately half that of their hosts, then models predict that both species will show cycles with a period approximately equal to the host generation time (Godfray & Hassell 1987, 1989). When hosts are common, many parasitoids develop, and these natural enemies suppress host abundances half a host generation later; this results in fewer parasitoids one whole host generation later and consequently leads to cyclic population dynamics. Generation cycles are seen in a variety of tropical and subtropical insects whose natural enemies have appropriate life histories and, although critical experiments have yet to be performed, they have been interpreted as resulting from this mechanism (Godfray & Hassell 1989; Reeve *et al.* 1994).

While there is considerable, if observational, evidence that generation cycles caused by the second mechanism occur in the field, there are few reports of generation cycles caused by the first mechanism outside of laboratory cultures. The models that have been developed to explore age-structured intraspecific interactions in *Tribolium* have incorporated specific details of the insect's biology, and it might be argued that only a narrow range of life histories or ecologies could produce this type of population dynamic. However, in figure 1 we describe a new model with few biological assumptions that displays this type of dynamic and suggests that a broad class of mechanisms in which later age classes harm or consume earlier life stages may produce generation cycles. We argue that this is the most probable explanation for regularities in a time-series of ladybeetle (Coccinellidae) abundances from Indonesia.

2. LADYBEETLE TIME-SERIES

Epilachna vigintioctopunctata (Fab.), the 28 spot ladybeetle, is a herbivorous coccinellid that feeds on solanaceous plants and is a pest of crops such as potato and aubergine (egg-plant). This beetle is common in Indonesia, where its

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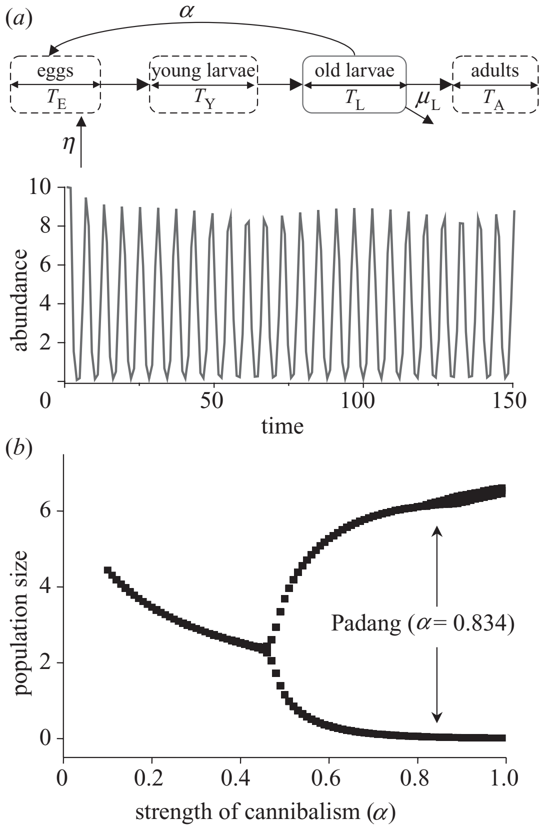

Figure 1. (*a*) Generation cycles caused by cannibalism. These dynamics can be described by a simple age-structured model of the form $\mathrm{d}L/\mathrm{d}t = R(t) - M(t) - u_L L(t)$, where $R(t) = \eta \exp\left(-\int_{t-T_E-T_Y}^{t-T_Y} \alpha L(x)\mathrm{d}x\right)$ and $M(t) = \eta \exp\left(-\int_{t-T_E-T_Y-T_L}^{t-T_Y-T_L} \alpha L(x)\mathrm{d}x\right)\exp(-\mu_L T_L)$; L is the density of old larvae, η is the population recruitment (oviposition) rate (which we assume to be independent of density as the reproductively active adult stage is relatively long-lived and constant with respect to the development time of the juvenile stages), μ_L is density-independent mortality rate, α is the rate of cannibalism, and T_E, T_Y and T_L are stage-specific development times (see insert for a schematic representation of the model). This simple model shows characteristic population cycles of approximately one generation in length driven by age-specific intraspecific predation (model parameters: $\eta = 10.5$, $\mu_L = 0.1$, $\alpha = 0.5$, $T_E = 1.0$, $T_Y = 2.0$ and $T_L = 1.0$). These cycles occur as intraspecific predation introduces a time-delayed feedback into the population: the density of the old larval stage is dependent on survival through the earlier stages (determined principally by the rate of cannibalism and the density of older larval stages). Depending on the rate of recruitment and the strength of cannibalism, this density-dependent feedback can lead to persistent population cycles. (*b*) Bifurcation diagram for the age-structured model. The dynamic structure of the model predicts stable equilibrium or generation-cycle dynamics depending on the strength of cannibalism (α). To compare model predictions and data, parameter estimates for the strength of cannibalism (α) were determined using a stochastic version of the age-structured model $E_{L[i]} = \exp(v)\int_t^{t+\tau}[R(t) - M(t) - u_L L(t)]$ $\mathrm{d}x$ (where noise (v, an independent identically distributed random variable) in the dynamics is assumed to be the result of environmental effects). This stochastic model is integrated over a fixed time-period ($t \rightarrow t + \tau$) equivalent to the census interval (τ) in the observed time-series, and fitted to the late juvenile instar dynamics of *Epilachna vigintioctopunctata* from Padang using an appropriate likelihood function $\left(Z(F) = \prod_{i=1}^{n}\left(\frac{1}{\sqrt{2\pi}}\right)\exp\left[-\frac{1}{2}\left(L_{[i]} - E_{L[i]}/\sigma\right)^2\right]\right)$.

long-term population dynamics have been studied in West Sumatra by Nakamura *et al.* (1988, 1990, 2001) and Inoue *et al.* (1993). We concentrate here on two time-series of beetle abundances from Padang and Sukarami; both sites are close to the equator and they are only 40 km apart, but Padang is in the lowlands (altitude 20 m) with mean monthly temperatures fluctuating between 26.7 °C and 27.5 °C and an annual rainfall of 4760 mm, while Sukarami is higher (altitude 930 m), cooler (20.8–21.4 °C) and drier (2900 mm). At both sites, the beetle's major food plant is a shrubby weed, *Solanum torvum*.

This ladybeetle has four juvenile stages, and, in Padang, development from egg hatch to adult takes *ca.* 23 days (Abbas *et al.* 1985). Following emergence, adults pass through a pre-reproductive period of *ca.* 11 days and are then reproductively active for their entire lifetime. Adult beetles can live for more than 80 days (mean ± s.e.: females, 57.7 ± 5.6 days; males, 87.3 ± 4.9 days) and females lay, on average, batches of approximately 13 (*ca.* 770/57.7) eggs per day over their lifetime. *Epilachna vigintioctopunctata* is highly cannibalistic when population density is high, and cannibalism can account for between 11% and 30% of total mortality in this species.

Population censuses of different life-history stages (egg, third-instar larvae, fourth-instar larvae, pupae, teneral adults and mature adults) were made at 3–7 day intervals over a period of 37 months from January 1982 to January 1985 at Padang and for almost 10 years between 1991 and 2000 at Sukarami. Full details of the field sites and sampling techniques are given in Nakamura *et al.* (1990, 2001). Life-history experiments in the laboratory have shown that there are differences in life histories between the sites. For example, at Padang the generation time is *ca.* 45 days and adult females live for 60 days, while at Sukarami generation time is 73 days and female longevity is 90 days (Abbas *et al.* 1985; N. Hasan, A. Hasyim, S. Nakano, S. Koji and K. Nakamura, unpublished data).

We looked for regularities in the data using time-series analysis implemented in S-Plus (in particular using the supplementary library 'pastecs', see http://www.sciviews.org/pastecs/). Because the intervals between data collection were not constant, we first regularized the time-series by linear interpolation with a 7-day interval. Partial autocorrelations (PACF) and periodograms were used to identify the frequency of population cycles. Periodograms were calculated using fast Fourier transforms and smoothed using (Daniell) moving averages.

Time-series for egg densities at Padang show a cyclic component ($\mathrm{PACF}_{\mathrm{lag}=49} = 0.165$) with a period of *ca.* 50 days (figure 2*a*,*b*). Adult densities from the same site show a slight tendency to cycle at the same frequency (figure 2*c*,*d*) and this was on the margins of significance ($\mathrm{PACF}_{\mathrm{lag}=49} = -0.139$). Densities of pupae and teneral adults also showed strong 50 day cycles (pupae: $\mathrm{PACF}_{\mathrm{lag}=49} = -0.182$; teneral adults: $\mathrm{PACF}_{\mathrm{lag}=49} = -0.218$), while cycles in the densities of third- and fourth-instar larvae were not as prominent or significant (third instar: $\mathrm{PACF}_{\mathrm{lag}=49} = -0.06$; fourth instar: $\mathrm{PACF}_{\mathrm{lag}=49} = 0.119$) (95% CI for the Padang time-series are obtained by adding or subtracting 0.134 from each of the PACF values). We suspect that the weaker cycles in these larval stages may be the result of difficulties in accurately

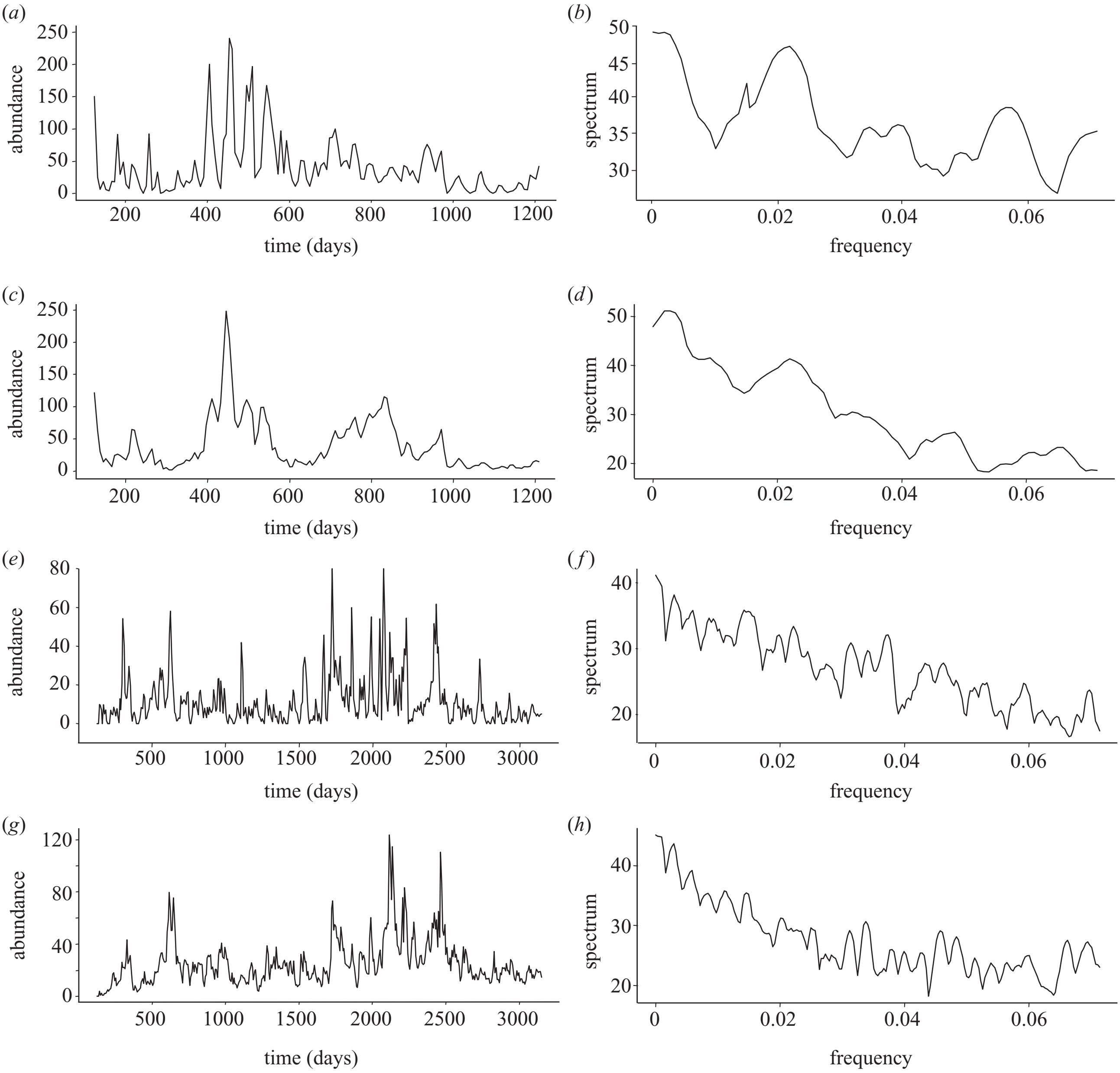

Figure 2. Time-series of *Epilachna vigintioctopunctata* at Padang and Sukarami, Indonesia. Paired time-series and power spectra for (*a*,*b*) egg abundance at Padang, (*c*,*d*) adult abundance at Padang, (*e*,*f*) egg abundance at Sukarami and (*g*,*h*) adult abundance at Sukarami. Generation cycles are prevalent in the egg and adult stages at Padang but not at Sukarami.

distinguishing between these stages. In contrast, at Sukarami, there is no evidence of any periodic dynamics in either the egg ($\mathrm{PACF}_{\mathrm{lag}=49} = 0.07$; figure 2*e*,*f*) or the adult ($\mathrm{PACF}_{\mathrm{lag}=49} = 0.03$; figure 2*g*,*h*) densities (95% CI for the Sukarami time-series are obtained by adding or subtracting 0.09 from each PACF value).

Our age-structured model shows either stable equilibrium or generation cycles depending on the strength of cannibalism (figure 1). We asked whether the observed dynamics were consistent with the predictions of this model. Using a likelihood-based approach (Bonsall & Hassell 2004) we attempted to fit the model to the ladybeetle time-series from Padang (we could not carry out a similar analysis for Sukarami because the time-series for different instars are not fully resolved). Although the populations show marked temporal variability, the model proved able to replicate the time-series with biologically reasonable parameter values (figure 1). Though not an independent test of the cannibalism hypothesis (as the parameters were estimated from the time-series itself), it shows the feasibility and consistency of this explanation.

3. DISCUSSION

The ladybeetle *E. vigintioctopunctata* shows strong generation cycles in juvenile but not adult life-history stages at a lowland site in Indonesia, though not at a nearby highland site. Given the limited set of alternative mechanisms for generation cycles (resource competition/cannibalism or predation), we suggest that the cycles are caused by asymmetric interactions between life-history stages of the same type that have been invoked to explain similar cycles in laboratory *Tribolium* cultures.

Is it possible that the generation cycles are caused by an interaction with a natural enemy rather than by intraspecific competition? We think this unlikely for three reasons: first, although parasitism is abundant, it occurs across all juvenile life stages (25% on eggs; 50–75% on pupae) – we know of no recorded natural enemy that has an appropriate life history (in particular developmental times approximately half, or one and a half times, that of the host) or responds in a sufficiently nonlinear way (Godfray & Hassell 1989) to the distribution of hosts. Second, in all the models and experimental systems showing natural-enemy-driven cycles *every* stage is predicted to show generation cycles (not just the juvenile stages as observed in this ladybeetle system). Finally, in models of host–parasitoid interactions the adult stage must be relatively short-lived compared with the developmental lag for generation cycles to appear (Godfray & Hassell 1989). If adults live too long then reproduction is no longer pulsed and any population cycles are expected to decay away. As noted, adult *E. vigintioctopunctata* have an oviposition rate of approximately 13 eggs per day and an average longevity of *ca*. 60 days (which is much longer than the development time of the immature stages of *ca*. 23 days).

Ladybeetles are well known to show varying degrees of intraspecific interference and cannibalism. This has been studied most frequently in predacious species where adults and larvae may consume younger stages, especially eggs, and less frequently pupae (Fox 1975; Iperti 1999; Dixon 2000). Phytophagous coccinellids in the subfamily Epilachninae are relatively poorly known, but previous studies have suggested that egg mortality resulting from cannibalism by older larvae may range from 11% (Padang) to 30% (Sukarami) and that, overall, intraspecific predation on eggs can cause 25% mortality (Nakamura *et al.* 1990).

Although cannibalism occurs at both sites, at present we have no explanation for why generation cycles are observed in the lowland but not the highland site. However, we predict that differences in the ecology of the beetle between the two sites cause greater intraspecific cannibalism and predation at Padang. Fully understanding the causes of the dynamics we have presented here will require further experimental and theoretical work, but our long-term time-series provide evidence for *Tribolium*-type generation cycles in a natural population.

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