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Inter-clutch interval and number of ovipositions in females of the damselfly *Ischnura graellsii* (Odonata: Coenagrionidae)

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ABSTRACT. *Oviposition behaviour was studied in a natural population of* I. graellsii *at O Rosal (NW Spain).*- For females seen ovipositing more than once, most oviposition episodes (40%) were separated by a one-day interval. This result is in agreement with previous laboratory work indicating that females of this species would maximize their lifetime egg production by minimizing inter-clutch interval, rather than by maximizing clutch size. Marked females oviposited 0-7 times during their lives, but no androchromotypic female was seen ovipositing more than once.

KEY WORDS. Odonata, Oviposition, Inter-clutch interval, Female colour polymorphism

In insect species that lay eggs in discrete clutches selection should favour the inter-clutch interval that maximizes lifetime egg production. Lifetime egg production is the product of the length of the reproductive span, the rate at which clutches are produced and the number of eggs in each clutch (Banks & Thompson, 1987). If oocytes mature continuously, clutch size will be proportional to the interval between successive ovipositions. The number of clutches is limited by the daily survival rate. When mortality is high, the probability of living long enough to lay a second clutch is low, and therefore females should maximize their reproductive success by laying eggs after the shortest inter-clutch interval. If mortality is low the inter-clutch interval may be longer.

In the damselfly *Coenagrion puella*, Banks & Thompson (1987) showed that females would maximize their lifetime egg production by minimizing the interval between clutches, rather than by maximizing clutch size, because a clutch that takes two days to mature is less than twice as big as one that takes one day to mature. In a laboratory study with females of *Ischnura graellsii*, I have shown that (excluding the first clutch) clutch size is positively related to the inter-clutch interval, but because maximum egg production is obtained by laying eggs at one-day intervals, I predicted that females should oviposit at short intervals in order to maximize their reproductive success (Cordero, 1991). My first aim in this note is to test this prediction with data obtained from a natural population. *I. graellsii* has three female colour phenotypes: one androchromotypic (male-like) and two gynochromotypics (*infuscans* and *aurantiaca* forms; Cordero, 1990). My second aim in this note is to present data on the number of ovipositions of the three female phenotypes, such data being

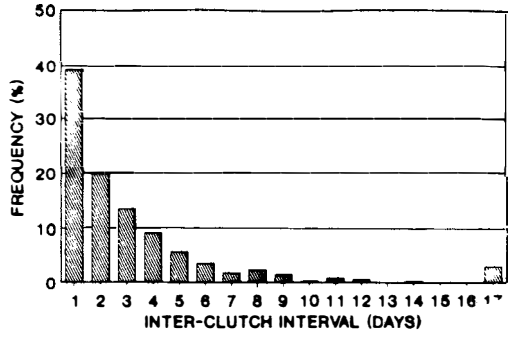

FIGURE 1. *Ischnura graellsii*. The percentage frequency distribution of inter-clutch intervals for all females seen ovipositing more than once.

[*Ischnura graellsii*. Distribución porcentual de los intervalos entre puestas para todas las hembras observadas en puesta más de una vez.]

important for the discussion of the maintenance of this colour polymorphism (Cordero, 1992).

During August and September 1990, I carried out a mark-recapture experiment in a natural population of *Ischnura graellsii* at O Rosal (Pontevedra, NW Spain, UTM: 29TNG1742). Females of this species typically oviposit alone on floating vegetation, although very rarely some females submerge completely alone to lay eggs on underwater vegetation (personal observations). A total of 2125 individuals (1055 females) were marked during 29 days (286 h of observation), in order to obtain estimates of population size, survivorship and mating success. The population inhabits an artificial pond of 300 m perimeter. I visited the pond daily from 11 August to 8 September, and walking slowly by the shore I recorded the identification code of each female seen ovipositing (usually by direct observation or using binoculars rather than by capture). Observations were made usually from 7 to 19 h (solar hour), while females oviposited between 9 and 17 h. Detailed methods and a description of the study area are in Cordero (1992). I did not record the duration of oviposition. Therefore I assume that all females seen ovipositing one or more times during the same morning laid one clutch of eggs in that day. The minimum inter-clutch interval that could be recorded was therefore one day.

Figure 1 presents the distribution of inter-clutch intervals for all females seen ovipositing on at least two different days. This figure was computed using 325 inter-clutch intervals recorded from 193 females. As predicted by Cordero (1991), most females (about 40% of all ovipositions) laid eggs at intervals of one day. The mean±SE inter-clutch interval was 2.85±0.14 days. On the other hand, taking into account that female daily survival rate was 0.788±0.835 during the period of study (life-table method; Cordero, 1992), the probability of living long enough to lay eggs with a longer inter-clutch interval is very low, and is accordingly a second selective force that could favour short inter-clutch intervals. Nevertheless, a significant number of clutches were laid after intervals longer than one day.

In *Coenagrion puella*, a species that oviposits in tandem (the male holds the female by the prothorax), most clutches (60%) were laid the day following the previous clutch (Banks & Thompson, 1987). *Enallagma hageni* oviposits underwater, a behaviour that can produce a mortality risk to females of 0.06 per oviposition bout, and that favours multiple mating by females, that are "rescued" by males on resurfacing (Fincke, 1986a). Unlike *I. graellsii* and *C. puella*, *E. hageni* lays eggs at intervals of 5.2±0.54 days (N=73 intervals, Fincke, 1986b). Female *E. hageni* could minimize this risk of mortality by minimizing the number of ovipositions, therefore producing large clutches at long intervals. Nevertheless daily survival rate of *E. hageni* females is very similar to that of *I. graellsii* (0.85; Fincke, 1986b). Therefore the longer inter-clutch interval of *E. hageni* is not to be explained by a lower survival rate during oviposition. The reason for this different behaviour might be related to the underwater oviposition of *Enallagma*. Miller

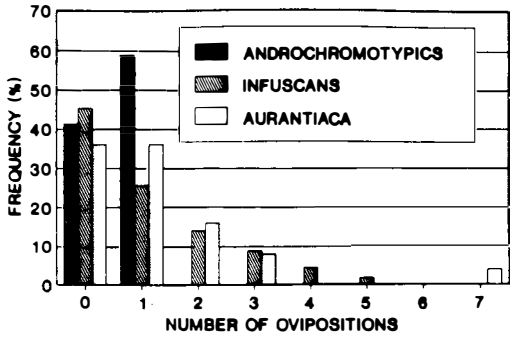

FIGURE 2. The number of ovipositions per female for three female phenotypes of *Ischnura graellsii*. Data from 155 females.

[Distribución del número de oviposiciones por hembra, para los tres fenotipos femeninos de *Ischnura graellsii*. Datos de 155 hembras.]

(1993) has shown that in *Enallagma cyathigerum* females can suffer oxygen shortage during prolongued underwater oviposition, and that as many as 98% of females may be trapped in the meniscus upon resurfacing. This behaviour might produce physiological stress favouring longer inter-clutch intervals. Studies on the oviposition behaviour and inter-clutch interval of other species are needed in order to clarify this question.

With regard to the female polymorphism of *I. graellsii*, for the subset of females whose mature lifespan was completed during the period of study (155 females; see Cordero, 1992), all phenotypes laid a similar number of clutches (androchromotypics: 0.59±0.51 (N=17) clutches, *infuscans*: 1.1±1.28 (113), *aurantiaca*: 1.20±1.53 (25); Kruskal-Wallis test=1.32, p=0.52), although no androchromotypic female was seen ovipositing more than once (fig. 2). Taking into account all females marked during this study, the ratio of ovipositing females (59:472:71 for androchromotypics, *infuscans* and *aurantiaca*) was not significantly different from the expected value (60:469:72) derived from the proportion of every phenotype in the population (110:855:132; X^2=0.076, p=0.96). Cordero (1992) showed that the mating success of androchromotypic females in this population was smaller than that of gynochromotypics (although the reported X^2 value in table 7 of that paper was miscalculated, the correct P-value being 0.091). The present results indicate that future studies of the maintenance of female colour polymorphism in this species should be undertaken by measuring the reproductive (oviposition) success of each female phenotype, because mating success alone could be a misleading measure of reproductive success.

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Resumen

Intervalo entre puestas y número de oviposiciones en las hembras del caballito del diablo Ischnura graellsii *(Odonata: Coenagrionidae).*

El comportamiento de oviposición de las hembras de *I. graellsii* ha sido estudiado mediante técnicas de marcaje y observación en una población natural en O Rosal (Pontevedra). La mayoría de las oviposiciones (40%) fueron realizadas con un intervalo de un día. Este resultado concuerda con las predicciones realizadas previamente a partir de estudios de laboratorio, que habían indicado que en esta especie las hembras maximizarían su éxito reproductivo minimizando el intervalo entre puestas, en lugar de maximizar el tamaño de cada puesta. Por

otra parte, las hembras marcadas fueron vistas en oviposición 0-7 veces, pero ninguna hembra androcromotípica fue observada en puesta más de una vez.

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