Maternal care and offspring behaviour in three theridiid species (Araneae, Theridiidae)

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Summary
Maternal care is widespread in theridiids. Theridion evexum Keyserling breaks the threads in the outer layer of the egg sac to allow its spiderlings to leave the sac. Achaearanea tesselata (Keyserling) and Anelosimus studiosus (Hentz) kill prey for their young spiderlings to feed upon. Occasionally, embryos of T. evexum die when their mother fails to break the threads of the egg sac properly, and spiderlings of A. tesselata and A. studiosus are sometimes killed when they are wrapped along with the prey when the adult spider is attacking prey. Offspring mortality is rare, suggesting that the attack behaviour is highly suppressed in spiderlings of social theridiids.

Introduction
Parental care is well known to enhance the fitness of offspring (Wilson, 1975; Avilés & Tufiño, 1998), particularly when species inhabit stressful environments that drastically affect their survivorship (Avilés & Gelsey, 1998; Miller &agnarsson, 2005). In spiders, maternal care is widespread within the family Theridiidae (Avilés, 1997; agnarsson, 2004, 2006), although the extent of maternal care behaviour varies greatly among genera and even among species in the same genus of this family (Bristowe, 1958; Foelix, 1996; agnarsson, 2004). It is generally assumed that parental care evolved and is maintained because the benefits outweigh the inherent costs of brood caring (Clutton-Brock, 1991; Bilde et al., 2007). In spiders maternal brood care reduces the female’s fecundity and survival (Avilés & Tufiño, 1998; Bilde et al., 2007). However, at least in some spiders, this cost is outweighed by a greater clutch size and offspring survival which increase the average individual fitness in social spiders (Avilés & Tufiño, 1998).

Maternal care in some theridiids ceases when the spiderlings emerge from the egg sac (e.g. Latrodectus spp.: Forster & Forster, 1973), but in social species maternal care includes the cohabitation of spiderlings with their mother for some time (Avilés, 1997; agnarsson, 2004, 2006). In some social species, in which new webs are established by single females which raise their offspring without the aid of others (Buskirk, 1981; Avilés & Bukowski, 2006), cohabitation extends until the spiderlings reach the third or fourth instar in the mother’s web (e.g. Theridion evexum Keyserling: Barrantes & Weng, 2007). Even in other species with a more complex social structure, in which colony members cooperate to build and maintain their web, and capture prey cooperatively, members of the colony share brood care (Avilés, 1997; Avilés & Salazar, 1999; agnarsson, 2006).

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Maternal care is displayed by theridiids in many different ways, including protecting the egg sac (Bristowe, 1958; Viera et al., 2007), capturing prey for the offspring to feed upon (Bristowe, 1958), regurgitating to the offspring (Bristowe, 1958; Foelix, 1996; Viera et al., 2005, 2007), and accumulating the bodies of dead prey before the emergence of the spiderlings from their egg sac (Barrantes & Weng, 2007, 2008). Here, we describe the maternal care and offspring behaviours and occasional mortality of offspring associated with maternal care in Theridion evexum, Achaearanea tesselata (Keyserling) and Anelosimus studiosus (Hentz).

Methods
Observations on the behaviour of adult and juvenile spiders of the three theridiid species were made in captivity, and in the field on the campus of the Universidad de Costa Rica (San José province) and in Parque del Este (Cartago province); both these sites are located at 1100–1300 m in the eastern portion of the Costa Rican Central Valley. Adult females of T. evexum (n=12) and A. tesselata (n=23) with their eggs and spiderlings were maintained in captivity as described in Barrantes & Weng (2006, 2007). The instars were numbered starting with the stage at which the spiderlings emerged from the egg sac (“first instar”) (one previous instar occurs within the egg sac), and females become adults possibly at the sixth or seventh instar. Webs with eggs and spiderlings (n=5) of A. studiosus were maintained on potted plants; 7 additional webs of adult spiders with egg sacs and/or spiderlings were observed in the field. The behaviour of adults and spiderlings was recorded using a Sony DCR-VX1000 digital camera equipped with close-up lenses; these recordings were complemented with naked-eye observations on captive spiders and in nature. Observations on manipulation of the egg sacs by adult females of T. evexum were made daily during the last week before the emergence of the spiderlings from the egg sac. Drawings are based on video images. Specimens of all three species have been deposited at the Museo de Zoología, Universidad de Costa Rica.

Results
Maternal care

Theridion evexum: Mature females of this species produced only one or two egg sacs during their life span (unpubl. data). The egg sac was maintained deep inside the retreat that is formed by folding a leaf (Barrantes & Weng, 2007), and spiderlings emerged approximately 20 days later. Mature females began to store the unconsumed bodies of dead prey about a week before the spiderlings emerged from the egg sac. Spiderlings then fed on both old and newly killed prey (Barrantes & Weng, 2007, 2008), and they usually remained in their mother’s web until their fourth instar outside the egg sac. During this time the adult spider continued to kill prey and to give them to the spiderlings to feed upon (n=12 spiders, >200 prey).