ORIGINAL PAPER

Costs, benefits, and plasticity of construction of nest defensive structures in paper wasps

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Abstract Various animals build nests with defensive structures to deter predation on offspring. Construction of nest defensive structures can reduce the probability of predation but will involve various costs. Here, we examined both the costs and benefits of the construction of a nest defensive structure in a paper wasp, *Polistes chinensis antennalis*, and clarify whether the paper wasp changes the level of defensive structures of nests depending on predation risk. A foundress (queen) of the paper wasp starts a colony in spring and maintains her nest alone until the emergence of workers. At this stage, pupae in the nests are sometimes preyed on by conspecifics of other nests. The intruder needs to break the cocoon, which seals the entrance of the cell, to extract the pupa from the cell. Foundresses often apply nest material (pulp) to the surface of cocoons in their nests. We found that pulp on a cocoon increased the time an intruder required to break the cocoon. This result shows that the pulp structure on cocoons helps to prevent predation on pupae. On the other hand, pulp on cocoons involved costs, including time required to collect pulp and being a potential obstacle to the emergence of workers from the cocoon. Additionally, we found that the amount of pulp on cocoons was greater in nests under higher predation risk than nests under lower predation risk. These results suggest that pulp on cocoons is a nest defensive structure, and foundresses adjusted the construction of the defensive structure depending on predation risk.

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Introduction

Many animal species build nests using surrounding and/or self-secreted materials and rear their offspring in the nests (Hansell 2005). Nests function to protect offspring from the adverse effects of the biotic and abiotic environments (Hansell 2005). In particular, nest predation is one of the greatest causes of reproductive failure (e.g., Ricklefs 1969; Fowler 1979; Strassmann et al. 1988). Therefore, animals build nests with various ornaments and structures (hereafter collectively referred to as defensive structures) to deter predation on offspring. For example, many birds (e.g., long-tailed tits, *Aegithalos caudatus*, and blue–gray gnatcatchers, *Polioptila caerulea*) cover nest exteriors with lichen, moss, and spider silk. This helps to camouflage nests from visually oriented predators (Collias and Collias 1984; Hansell 1996). Common waxbills, *Estrilda astrild*, and great crested flycatchers, *Myiarchus crinitus*, place carnivore scat and snake skins, respectively, in, on, and around their nests, which act as an olfactory camouflage (Schuetz 2004; Medlin and Risch 2006). The mud wasp, *Paralastor* sp., builds a nest with a funnel-shaped entrance, which prevents predators entering the nest (Smith 1978).

On the other hand, building behavior involves costs in time and energy to collect, process, and assemble nest materials (Withers 1977; Collias 1986; Stanley 2002). In addition, defensive structures could harm the development of the offspring (Mayer et al. 2009; Prokop and Trnka 2011). Therefore, animals should avoid excessively constructing defensive structures.

Generally, predation risk varies spatially and temporally (Lima and Bednekoff 1999; Sih 2005; Creel and Winnie

2005), and therefore, animals are predicted to adjust the construction of defensive structures depending on predation risk. Many previous studies have demonstrated the antipredator function (benefits) of nest defensive structures in various animals (Martin 1992; Hansell 1996; Schuetz 2004; Medlin and Risch 2006) and suggested that the inter-specific variation of nest architectures is adaptation to predators (Jeanne 1975). However, those studies have overlooked the plasticity in the construction of nest defensive structures, and therefore, it is not known whether individuals change the construction of defensive structures of nest depending on predation risk. Because plasticity in antipredator traits plays an important role in predator–prey interactions (Lima et al. 2003; Sih 2005; Caro 2005), we need to investigate not only the defensive function of nest structures but also whether the structures are adjusted to predation risk to understand the interactions between nest predators and nesting animals.

The purpose of this study was to examine both the costs and benefits of the construction of a nest defensive structure and then clarify whether construction of the defensive structure was adjusted to predation risk. We focused on the nest structure of a paper wasp, *Polistes chinensis antennalis*, whose immatures are often preyed on by conspecifics from other nests (Kasuya et al. 1980; Furuichi and Kasuya 2013a).

A foundress (queen) of *P. chinensis* initiates a new colony solitarily in spring (Miyano 1980). The foundress builds a nest with pulp, which is a mixture of plant fiber and oral secretion of the foundress (Kudô et al. 1998; Kudô 2000). The foundress maintains a nest alone until the first workers emerge (Kasuya 1983a, b). At this stage, nests were often attacked by conspecific foundresses of other nests (Kasuya et al. 1980). The intruder flies to a nest whose owner is absent, extracts a larva from the cell, takes it back to her nest, and feeds her larvae with it (Kasuya et al. 1980). The owner can repel the attack by the intruder if she is on her nest (Kasuya 1983a). However, the foundress needs to leave the nest to gather resources such as water, pulp, and food for her larvae (Kasuya 1983a, b; Furuichi and Kasuya 2013b). Therefore, the foundress cannot completely prevent predation by intruders.

Intruders mainly prey on larvae, but recently, we found that sometimes they also prey on pupae (see Movie 1 of the "Electronic supplementary material"). Predation on pupae will delay the emergence of the first workers and extend the most vulnerable period when a solitary foundress maintains the nest (Miyano 1980). Therefore, predation on pupae has a severe negative effect on the nesting success of the foundresses. Foundresses should use additional ways to surely prevent predation on pupae.

The larva of a paper wasp spins a cocoon to seal the entrance of its cell before pupation (Fig. 1). Therefore, intruders need to break the cocoon to extract the pupa from the cell (see Movie 1 of the "Electronic supplementary material").

Fig. 1 **a** A nest of *P. chinensis*, **b** the frontal image of cocoons in the nest, and **c** diagrammatic representation of cocoons of the nest. The *solid area* represents pulp applied. **d** A diagram showing a longitudinal section of a cell containing a pupa

In *P. chinensis*, foundresses often apply pulp to the surface of their cocoons (Fig. 1). They will reinforce the cocoon by the application of pulp, and pulp on the cocoon will increase the time that intruders require to break the cocoon. If a foundress returns to the nest when the intruder is still breaking a cocoon, the foundress can chase off the intruder before the intruder preys on the pupa (Kasuya 1983a). That is, increasing the time required for breaking the cocoon increases the probability of preventing predation on pupae and is an effective means of defense. Pulp that is applied to cocoons is predicted to function to prevent predation on pupae.

On the other hand, the application of pulp to cocoons involves time and energy costs. In addition, there are two other possible costs. First, workers that have eclosed from pupae need to break the cocoon. The body of a worker that has just eclosed is still soft, and therefore, pulp on the cocoon is a possible obstacle to emergence from it. Second, pulp contains a significant amount of protein derived from the oral secretion of the foundress, a valuable and limited resource derived from ingested prey (Kudô 2000, 2002). Therefore, applying a large amount of pulp to cocoons could decrease the amount of pulp available for the construction of the body of a nest. For these reasons, foundresses should not apply an excess of pulp to cocoons. Foundresses, therefore, are predicted to adjust the amount of pulp on cocoons depending on predation risk.

In this study, first, to clarify the defensive function of pulp on cocoons, we examined whether pulp on the cocoon increased the time intruders required to break the cocoon. Second, to clarify whether there were costs of pulp application to cocoons in addition to the expenditure of time and energy, we examined whether pulp on a cocoon was an obstacle to the emergence of workers from the cocoons and whether the investment of pulp applied to cocoons decreased the amount of pulp available for the construction of the body of the nest. Third, to clarify whether foundresses adjusted the construction of the nest structure to predation risk, we examined whether foundresses applied a greater amount of pulp to cocoons under a higher risk of nest predation.

Materials and methods

Study species and site

P. chinensis is a eusocial wasp with an annual life cycle. Overwintering foundresses emerge in spring and begin nest construction and brood rearing alone (Kasuya 1983a, b). Workers emerge from late spring to summer (Miyano 1980). Foundresses mainly prey on lepidopteran larvae (Suzuki 1978; Kasuya 1980), but often attack conspecific nests (Kasuya et al. 1980; Kasuya 1983a).

This study was conducted in a grassland area (approximately 0.54 ha) of Kashiihama in Fukuoka, Japan (33°39′27″ N, 130°25′37″ E), from May 9 to June 15, 2011. Forty-seven nests of *P. chinensis* were found. We marked foundresses individually with enamel paint (Opaque Color, Teranishi Chemical Industry, Osaka, Japan) and measured their head widths with a digital caliper (CD-15B, Mitutoyo Corporation, Kanagawa, Japan) to the nearest 0.01 mm.

Measurement method of the amount of pulp on a cocoon

We photographed each cocoon using a digital camera (Optio W80, Pentax Ricoh Imaging Company, Tokyo, Japan). The amount of pulp on a cocoon (dimensionless value) was calculated as the ratio of the area of pulp on a cocoon to the frontal area of the cocoon, both determined using the image analysis software ImageJ ver.1.46r (Abramoff et al. 2004). Because the dry weight of pulp on a cocoon was strongly positively correlated with the ratio of the pulp area ($r=0.94$, $t=11.1$, $df=17$, $P<0.0001$, $N=19$; S. Furuichi, unpublished data), we used the ratio of the pulp area as an index of the amount of pulp.

Field observations

At the study site, we started the observation of each nest when only eggs and/or small larvae (the first and second instar larvae) were present in the nest and continued it until emergence of the first worker from the nest. We photographed each nest at 1700 h every day using a digital camera to record the states of the nest. From the images, we recoded the number and arrangement of cells in a nest, the contents of cells (empty, egg, first to fifth instar larva, and pupa), and the amount of pulp on each cocoon. We calculated two indices of the amount of pulp on cocoons in a nest: (1) the total amount of pulp on cocoons in a nest (dimensionless value), which was the sum of the amount of pulp on a cocoon of all the cocoons in a nest, and (2) the mean amount of pulp on a cocoon in a nest (dimensionless value). There was a positive, high correlation between the total amount of pulp on cocoons and the mean amount of pulp on a cocoon in a nest ($r=0.86$, $t=5.69$, $df=11$, $P=0.0001$, $N=13$), and therefore, we used only the total amount of pulp on cocoons in the analyses. We recorded the number of predation events by conspecifics as an index of predation risk from the daily data on the states of nests. We defined a sudden disappearance of larvae or pupae as predation by conspecifics because it never arose unless predation by conspecifics occurred. Nineteen nests were abandoned by the foundresses before the emergence of workers, and we were able to observe 13 nests until the emergence of workers. The data from these 13 nests were used in the analyses.

Predation experiment

To observe predation on pupae by conspecifics, we conducted a predation experiment from May 25 to June 5. We collected 10 nests with cocoons from the study site and recorded the amount of pulp on each cocoon. We removed the foundress, eggs, and larvae from the nest and then returned the nest to where it had been at the study site. Nests were placed and monitored from 0800 to 1600 h. Nests were monitored by video cameras (DCR-SR87, Sony, Tokyo, Japan), which were placed approximately 1 m from the nest. From the recorded images of predation by conspecifics, we recorded the identity of the intruder, the identity of the pupa preyed on, and the time required for breaking a cocoon (in seconds). The time required for breaking a cocoon was defined as the time from when the intruder bit the cocoon to when she completely pulled the pupa out of the cell.

Emergence-from-cocoon experiment

We collected five nests with cocoons from the study site on June 5 and recorded the amount of pulp on each cocoon. To observe the emergence of workers from the cocoons, we removed the foundress, eggs, and larvae from the nest and then placed the nest in the laboratory at 25 °C and 60 % relative humidity. Nests were constantly monitored by the video cameras, which were placed approximately 1 m from the nest. For monitoring, we kept the laboratory lit. From the

recorded images of the emergence of workers from the co-coons, we recorded the identity of the emerging worker and the time required to emerge from a cocoon (in seconds). The time required to emerge from a cocoon was defined as the time from the appearance of a part of the mandibles of the emerging worker to the complete appearance of its body from the cell. In addition, we measured the head width of workers with a digital caliper to the nearest 0.01 mm.

Data analyses

First, we investigated whether pulp on cocoons functions to prevent predation on pupae. We examined whether the amount of pulp on a cocoon affected the time required for breaking a cocoon, using the data of the predation experiment and using generalized linear mixed models (GLMMs) with a Gaussian error structure and an identity link. In the model, the identity of the attacked nest and the identity of the attacking conspecific were incorporated as random effects. Because the body size of the intruders (confounding factor) possibly affects the time required for breaking a cocoon, it was also incorporated as an explanatory variable in the model to adjust for the confounding effect.

Second, we investigated the costs of pulp application. To investigate whether pulp on a cocoon was an obstacle to the emergence of a worker from the cocoon, we examined whether pulp on a cocoon increased the time required for emergence from a cocoon, using the data of the emergence-from-cocoon experiment and using GLMMs with a Gaussian error structure and the identity link. In the model, the identity of the nest was incorporated as a random effect. Because the body size of the worker (confounding factor) possibly affects the time required for emerging from a cocoon, it was also incorporated as an explanatory variable in the model to adjust for the confounding effect. To investigate whether the investment of pulp in application to cocoons decreases the amount of pulp available for the construction of the body of the nest, we examined whether the total amount of pulp on cocoons affected the number of cells in the nest. In this analysis, we used the data of the field observation and used generalized linear models (GLMs) with a Poisson error structure and the log link. We used the total amount of pulp on cocoons and the number of cells in the nest on the seventh day after the first cocoon was spun in the nest. Because predation risk possibly affects the number of cells, the index of predation risk (confounding factor) was also incorporated as an explanatory variable in the model to adjust for the confounding effect.

Third, we investigated whether foundresses adjusted the amount of pulp on cocoons depending on predation risk. We examined whether predation risk affected the total amount of pulp on cocoons in a nest using field observation data and using GLMs with a Gaussian error structure and the identity link. In this analysis, we used the amount of pulp in a nest on the seventh day after the first cocoon was spun in the nest. Because the number of old larvae (fourth and fifth instar larvae) possibly affected the amount of pulp on cocoons, the number of old larvae (confounding factor) was also incorporated as an explanatory variable in the models to adjust for the confounding effect. When many old larvae, which consume a large amount of food, are present in a nest, the foundress of the nest will need to spend more time foraging and not spend enough time collecting pulp, possibly resulting in a decrease in the amount of pulp on cocoons.

To examine the significance of the explanatory variables, we conducted a likelihood ratio test in all the analyses. All the tests were two-tailed, and the level of significance was 0.05. All the analyses were performed with the statistical software R ver.2.15.1 (R Development Core Team 2012).

Results

Field observations

During the field observations, predation by conspecifics occurred 19 times. Of them, 16 were predation on larvae and 3 on pupae. The mean number±SD of predation events per nest was 1.47 ± 1.33 and ranged from 0 to 3. Of all the 13 nests observed, application of pulp to cocoons was found in 12 nests. Pulp was applied to a cocoon to cover it partially rather than entirely.

Defensive function of pulp application

In the predation experiment, we observed 19 predation events by 12 intruders. Intruders required 144.4 ± 119.3 s (mean±SD) to break a cocoon. The time required to break a cocoon increased significantly ($\beta \pm SE = 476.49 \pm 64.15$, $\chi^2 = 55.2$, $P < 0.0001$) as the amount of pulp on the cocoon increased (Fig. 2). This relationship appeared to be driven by one datum (the point placed on the right of Fig. 2), but removal of this datum still resulted in a significant relationship ($\beta \pm SE = 337.0 \pm 53.0$, $\chi^2 = 40.5$, $P < 0.0001$).
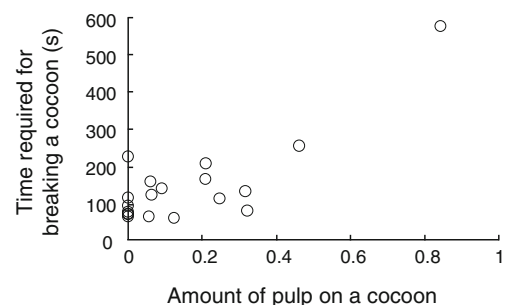
Fig. 2 The relationship between the amount of pulp on a cocoon and the time that an intruder required for breaking the cocoon. An *open circle* represents a cocoon

Costs of pulp application

In the emergence-from-cocoon experiment, we observed the emergence of 16 workers. No worker was injured or failed to emerge from cocoons owing to pulp on a cocoon. Workers required a significantly longer time ($\beta \pm SE = 4{,}021 \pm 1{,}475$, $\chi^2 = 7.43$, $P = 0.006$) to emerge when the amount of pulp on a cocoon was greater (Fig. 3). The mean number $\pm SD$ of cells in a nest was 37.1 ± 5.3. The total amount of pulp on cocoons did not significantly affect the number of cells ($\beta \pm SE = 1.83 \pm 2.81$, $\chi^2 = 0.43$, $P = 0.51$).

Adjustment of pulp application to predation risk

The total amount $\pm SD$ of pulp on cocoons in a nest was 0.93 ± 0.79, on average, and ranged from 0 to 2.92. The nest without pulp on cocoons did not suffer predation during the observation. The total amount of pulp on cocoon in a nest was significantly higher in the nests that suffered predation more frequently (Fig. 4; $\beta \pm SE = 0.38 \pm 0.16$, $\chi^2 = 5.97$, $P = 0.01$).

Discussion

Pulp on a cocoon increased the time that intruders required to break the cocoon (Fig. 2). This shows that pulp on a cocoon helps to prevent predation on pupae. Increasing the time required for breaking the cocoon increases the likelihood that the owner returns to the nest before the intruder finishes removing the pupa (Kasuya 1983a). On the other hand, to construct the pulp structure on cocoons, foundresses need to spend time collecting pulp. In the nests observed in the field, the amount of pulp applied to cocoons (the total amount $\pm SD$ of pulp on cocoons in a nest) was 0.46 ± 0.39 mg ($N = 13$), on average, and up to 1.44 mg (the dry weight of the total amount of pulp on cocoons in a nest was estimated by regression analysis; S. Furuichi, unpublished data). The mean amount $\pm SD$ of pulp that foundresses gathered in one pulp-gathering trip was 0.39 ± 0.09 mg ($N = 4$ foundresses, dry weight; S.

Furuichi, personal observation). Therefore, it is estimated that foundresses conducted pulp-gathering trips 1.2 times, on average, and up to 3.7 times to construct the pulp structure on cocoons. Because the time of one pulp-gathering trip was 141.1 ± 62.2 s (mean $\pm SD$, $N = 10$ foundresses; S. Furuichi, personal observation), foundresses were estimated to spend 169.3 s, on average, and up to 522.1 s to construct the pulp structure on cocoons.

Pulp on cocoons possibly becomes the obstacle to the emergence of workers from the cocoon. We found that pulp on a cocoon increased the time that workers required for emerging from cocoons (Fig. 3). This suggests that pulp on cocoons has the potential to injure the emerging workers and lead to failure of emergence from the cocoon. In our study, however, no worker failed to emerge or was injured owing to pulp on cocoons. Although pulp on a cocoon is a possible obstacle to the emergence from cocoons, the adverse effect would be small.

There is a possibility that the amount of pulp available is limited because pulp contains a significant amount of protein, a valuable and limited resource (Kudô 2000, 2002). Under such conditions, if a wasp was to apply a large amount of pulp to cocoons, it would lead to a decreased amount of pulp available for the construction of the body of the nest. However, in the present results, the investment of pulp in application to cocoons did not have a significant effect on the number of cells in the nest. The amount of pulp applied to cocoons might only be a small part of pulp available.

This study suggests that application of pulp to cocoons not only has a benefit of preventing predation on pupae but also involves costs. In the field observation, we found that foundresses applied a larger amount of pulp to cocoons when predation risk was high and a smaller amount of pulp to cocoons when predation risk was low (Fig. 4). This suggests that pulp on cocoons is a nest defensive structure, and foundresses adjust the amount of pulp on cocoons depending on predation risk. When predation risk is high, foundresses will gain a high benefit from applying a large amount of pulp to cocoons, and the benefit will outweigh the cost. In contrast, when predation risk is low, even if foundresses apply a large
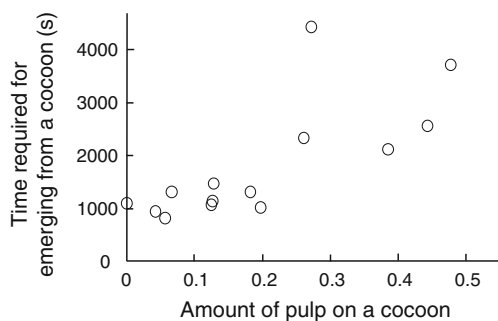

Fig. 3 The relationship between the amount of pulp on a cocoon and the time that a worker required for emerging from the cocoon. An *open circle* represents a cocoon
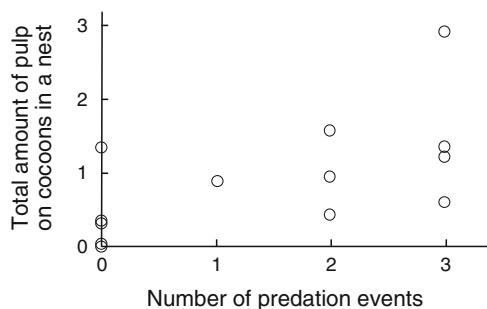

Fig. 4 The relationship between predation risk and the total amount of pulp on cocoons in a nest. An *open circle* represents a nest

amount of pulp to cocoons, the benefit from pulp application will be small, and the cost will outweigh the benefit. Foundresses will adjust the amount of pulp on cocoons to maximize the net benefit from pulp application.

Pulp application on cocoons is possibly conditional not only on predation risk but also on prey availability. If it takes more time to find prey, the pupae are necessarily exposed to the danger of predation for a longer time. The variation in the amount of pulp on cocoons in this study possibly resulted from the variation in the prey availability. However, the prey availability of field foundresses of this species has typically been estimated to be very low (Suzuki 1978; Kasuya 1983a, b), and therefore, the prey availability unlikely caused the variation in the amount of pulp on cocoons among nests in this study (though, unfortunately, we did not investigate the prey availability in this study).

In the field observation, we found that predation on larvae was far more common than on pupae. The rarity of predation on pupae in the field could be interpreted in two ways. First, the cocoons and pulp structures on cocoons are highly successful in deterring predation by conspecifics. Second, intruders prefer larvae, which intruders can rob in a shorter time, to pupae. In fact, when attacking nests with larvae and pupae, intruders often contact and ignore the capped brood (S. Furuichi, personal observation). The cocoons and pulp on cocoons would effectively prevent predation on pupae.

Defense of offspring through nest structures can be divided into two stages (Edmunds 1974): "primary defense" that reduces the likelihood of detection of nests by predators (e.g., camouflage; Collias and Collias 1984; Hansell 1996) and "secondary defense" that reduces the likelihood of successful predation after detection of nests by predators (e.g., mechanical protection; Martin 1992; Smith 1995; Leader and Yom-Tov 1998). Pulp on cocoons is a defensive structure that increases the time required for predation and decreases the probability of successful predation. Therefore, it has the function of a secondary defense. Previous studies reported that the application of pulp to cocoons occurs in many paper wasps that make exposed nests (Jeanne 1972; Kojima 1982; Spradbery and Kojima 1989; Hagiwara and Kojima 1994). These studies interpreted this behavior as camouflaging the nests by making the conspicuous white cocoons less obvious (Jeanne 1972; Kojima 1982; Spradbery and Kojima 1989; Hagiwara and Kojima 1994). That is, these studies inferred that pulp on cocoons has a primary defensive function. In *P. chinensis*, pulp on cocoons may also have such a function in addition to secondary defense.

Previous studies focused only on demonstrating the function of nest structures (Martin 1992; Hansell 1996; Schuetz 2004; Medlin and Risch 2006). Therefore, although many studies have investigated the function of nest structures, none had examined whether individuals changed the construction of nest structures based on predation risk. To our knowledge,

this study is the first to suggest that individuals can adjust a nest defensive structure to predation risk. Various animals build nests to protect offspring against predators, and the costs of building nests are common (Hansell 2005). Adjusting nest structures to predation risk could be prevalent in nesting animals. Furthermore, the structures that animals build are not only nests that protect offspring. A number of different animals build structures to protect themselves against predators (Hansell 2005). For example, the larvae of many caddisfly species build their own portable cases made of organic and/or mineral particles that are cemented with the silk that they secrete (Boyero et al. 2006). The larvae of several species of leaf beetle build shelters using their own waste materials (Eisner and Eisner 2000; Brown and Funk 2010). Many spider species build their own shelter using self-secreted silk (Manicom et al. 2008). Constructing the structures is considered to involve costs (Venner et al. 2003; McKie 2004; Mondy et al. 2011), and the animals will adjust them depending on predation risk. Many theoretical and empirical studies show that the changes in behavior and morphology in response to predation risk play an important role in predator–prey interactions (e.g., Lima et al. 2003; Sih 2005; Caro 2005). Similarly, the changes in architectural structure in response to predation risk will have a significant effect on predator–prey interactions. Our results suggest that, to understand the interactions between predators and the animals, we need to investigate not only the defensive function of the architectural structures but also how the structures are adjusted to predation risk.

References

Abramoff MD, Magelhaes PJ, Ram SJ (2004) Image processing with ImageJ. Biophotonics Int 11:36–42

Boyero L, Rincón PA, Bosch J (2006) Case selection by a limnephilid caddisfly [*Potamophylax latipennis* (Curtis)] in response to different predators. Behav Ecol Sociobiol 59:364–372

Brown CG, Funk DJ (2010) Antipredatory properties of an animal architecture: how complex faecal cases thwart arthropod attack. Anim Behav 79:127–136

Caro T (2005) Antipredator defenses in birds and mammals. The University of Chicago Press, Chicago

Collias N (1986) Engineering aspects of nest building by birds. Endeavour 10:9–16

Collias NE, Collias EC (1984) Nest building and bird behaviour. Princeton University Press, Princeton

Creel S, Winnie JA (2005) Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Anim Behav 69:1181–1189

Edmunds M (1974) Defence in animals: a survey of anti-predator defences. Longman, Harlow

Eisner T, Eisner M (2000) Defensive use of a fecal thatch by a beetle larva (*Hemisphaerota cyanea*). Proc Natl Acad Sci USA 97:2632–2636

Fowler LE (1979) Hatching success and nest predation in the green sea turtle, *Chelonian mydas*, at Tortuguero, Costa Rica. Ecology 60:946–955

Furuichi S, Kasuya E (2013a) Hurrying foragers fail to choose the best prey item: prey choice in paper wasps depredating conspecific nests. Ethology 119:786–792

Furuichi S, Kasuya E (2013b) Mothers vigilantly guard nests after partial brood loss: a cue of nest predation risk in a paper wasp. Ecol Entomol 39:339–345

Hagiwara Y, Kojima J (1994) Options in construction behavior for *Polistes mandarinus* Saussure nesting on Japanese cedar twigs (Hymenoptera: Vespidae). J Kansas Entomol Soc 67:126–128

Hansell MH (1996) The function of lichen flakes and white spider cocoons on the outer surface of birds' nests. J Nat Hist 30:303–311

Hansell MH (2005) Animal architecture. Oxford University Press, Oxford

Jeanne RL (1972) Social biology of the Neotropical wasp *Mischocyttarus drewseni*. Bull Mus Comp Zool 144:63–150

Jeanne RL (1975) The adaptiveness of social wasp nest architecture. Q Rev Biol 50:267–286

Kasuya E (1980) Behavioral ecology of Japanese paper wasps, *Polistes* spp. (Hymenoptera: Vespidae) I. Extranidal activities of *Polistes chinensis antennalis*. Res Popul Ecol 22:242–254

Kasuya E (1983a) Behavioral ecology of Japanese paper wasps, *Polistes* spp. II. Ethogram and internidal relationship in *P. chinensis antennalis* in the founding stage (Hymenoptera: Vespidae). Z Tierpsychol 63:303–317

Kasuya E (1983b) Behavioral ecology of Japanese paper wasps, *Polistes* spp. III. Decision making by *P. chinensis antennalis* foundresses at the departure from nests. J Ethol 1:15–21

Kasuya E, Hibino Y, Itô Y (1980) On "intercolonial" cannibalism in Japanese paper wasps, *Polistes chinensis antennalis* Pérez and *P. jadwigae* Dalla Torre (Hymenoptera: Vespidae). Res Popul Ecol 22:255–262

Kojima J (1982) Nest architecture of three *Ropalidia* species (Hymenoptera: Vespidae) on Leyte Island, the Philippines. Biotropica 14:272–280

Kudô K (2000) Variable investments in nests and worker production by the foundresses of *Polistes chinensis* (Hymenoptera: Vespidae). J Ethol 18:37–41

Kudô K (2002) Daily foraging activities and changes of allocation pattern of proteinaceous resources in pre-emergence laboratory foundresses of *Polistes chinensis* (Hymenoptera; Vespidae). Sociobiology 39:243–257

Kudô K, Yamane S, Yamamoto H (1998) Physiological ecology of nest construction and protein flow in pre-emergence colonies of *Polistes chinensis* (Hymenoptera Vespidae): effects of rainfall and microclimates. Ethol Ecol Evol 10:171–183

Leader N, Yom-Tov Y (1998) The possible function of stone ramparts at the nest entrance of the blackstart. Anim Behav 56:207–217

Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am Nat 153:649–659

Lima SL, Mitchell WA, Roth TC (2003) Predators feeding on behaviourally responsive prey: some implications for classical models of optimal diet choice. Evol Ecol Res 5:1083–1102

Manicom C, Schwarzkopf L, Alford RA, Schoener TW (2008) Self-made shelters protect spiders from predation. Proc Natl Acad Sci USA 105:14903–14907

Martin SJ (1992) Colony defence against ants in *Vespa*. Insect Soc 39:99–111

Mayer PM, Smith LM, Ford RG, Watterson DC, McCutchen MD, Ryan MR (2009) Nest construction by a ground-nesting bird represents a potential trade-off between egg crypticity and thermoregulation. Oecologia 159:893–901

McKie BG (2004) Disturbance and investment: developmental responses of tropical lotic midges to repeated tube destruction in the juvenile stages. Ecol Entomol 29:457–466

Medlin EC, Risch TS (2006) An experimental test of snake skin use to deter nest predation. Condor 108:963–965

Miyano S (1980) Life tables of colonies and workers in a paper wasp, *Polistes chinensis antennalis*, in central Japan (Hymenoptera: Vespidae). Res Popul Ecol 22:69–88

Mondy N, Cathalan E, Hemmer C, Voituron Y (2011) The energetic costs of case construction in the caddisfly *Limnephilus rhombicus*: direct impacts on larvae and delayed impacts on adults. J Insect Physiol 57:197–202

Prokop P, Trnka A (2011) Why do grebes cover their nests? Laboratory and field tests of two alternative hypotheses. J Ethol 29:17–22

Development Core Team R (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ricklefs RE (1969) An analysis of nesting mortality in birds. Smith Contr Zool 9:1–48

Schuetz JG (2004) Common waxbills use carnivore scat to reduce the risk of nest predation. Behav Ecol 16:133–137

Sih A (2005) Predator–prey space use as an emergent outcome of a behavioral response race. In: Barbosa P, Castellanos I (eds) Ecology of predator–prey interactions. Oxford University Press, Oxford, pp 240–255

Smith AP (1978) An investigation of the mechanisms underlying nest construction in the mud wasp *Paralastor* sp. (Hymenoptera: Eumenidae). Anim Behav 26:232–240

Smith FA (1995) Den characteristics and survivorship of woodrats (*Neotoma lepida*) in the eastern Mojave Desert. Southwest Nat 41:366–372

Spradbery JP, Kojima J (1989) Nest descriptions and colony populations of eleven species of *Ropalidia* (Hymenoptera, Vespidae) in New Guinea. Jpn J Entomol 57:632–653

Stanley TR (2002) How many kilojoules does a black-billed magpie nest cost? J Field Ornithol 73:292–297

Strassmann JE, Queller DC, Hughes CR (1988) Predation and the evolution of sociality in the paper wasp *Polistes bellicosus*. Ecology 69:1497–1505

Suzuki T (1978) Area, efficiency and time of foraging in *Polistes chinensis antennalis* Pérez (Hymenoptera, Vespidae). Jpn J Ecol 28:179–189

Venner S, Bel-Venner MC, Pasquet A, Leborgne R (2003) Body-mass-dependent cost of web-building behavior in an orb weaving spider, *Zygiella x-notata*. Naturwissenschaften 90:269–272

Withers PC (1977) Energetic aspects of reproduction by the cliff swallow. Auk 94:718–725