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NEST LIGHT ENVIRONMENT AND THE POTENTIAL RISK OF COMMON CUCKOO (*CUCULUS CANORUS*) PARASITISM

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ABSTRACT.—Brood parasitism represents a significant cost in reproduction; thus, natural selection should favor the evolution of host defenses, which in turn may favor evolution of more sophisticated techniques by the parasite to overcome host defenses. These host defenses include egg rejection, attacking parasites near the nest, and avoiding parasitism by concealing nest sites. In all these antiparasitism strategies, nest light environment may play an important role. In the present study, the risk of Common Cuckoo (*Cuculus canorus*) parasitism for the Great Reed Warbler (*Acrocephalus arundinaceus*) was modeled in relation to the *in situ* nest light environment, from far ultraviolet (UV) to infrared (IR) radiation (280–1,100 nm), and nest situation and structure. The percentage of photosynthetically active radiation (PAR) plus IR radiation (400–1,100 nm) falling on the nest, maximum nest width, and distance between the nest and the nearest active conspecific neighbor were significantly related to the risk of parasitism. Photosynthetically active radiation alone explained 65% of variation in parasitism risk in the final model. Although solar radiation levels in nests were low (<4% for UV-B and UV-A radiation, 5% for PAR, and 22% for PAR plus IR radiation when cloudless), UV-B, UV-A, and visible-plus-IR radiation levels were significantly lower in nonparasitized nests. These findings provide the first evidence of a relationship between parasitism risk and nest concealment related to microhabitat light environment, with brighter nests suffering a higher risk of parasitism. Received 12 October 2005, accepted 4 June 2006.

Key words: *Acrocephalus arundinaceus*, antiparasitism defenses, brood parasitism, Common Cuckoo, *Cuculus canorus*, Great Reed Warbler, light environment, ultraviolet radiation.

Nest Light Environment and the Potential Risk of *Cuculus canorus* Parasitism

RESUMEN.—El parasitismo de cría representa un coste importante en la reproducción, por lo que la selección natural debería favorecer la evolución de las defensas del hospedador, que así mismo favorecerían la evolución de técnicas más sofisticadas por parte del parásito para superarlas. Estas defensas del hospedador incluyen el rechazo de huevos, el ataque a individuos parásitos cercanos al nido, y el ocultamiento de los nidos para evitar el parasitismo. En todas estas estrategias antiparasitarias, el ambiente lumínico en el nido puede jugar un papel importante. En el presente estudio se modela el riesgo de parasitismo del Cuco Común (*Cuculus*

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canorus) sobre el Carricero Tordal (*Acrocephalus arundinaceus*), con relación al ambiente lumínico *in situ*, desde la región ultravioleta (UV) hasta la infrarroja (IR) (280-1,100 nm), y a la situación y estructura del nido. El porcentaje de radiación fotosintéticamente activa (PAR) más radiación IR (400-1,100 nm) que llega al nido, la anchura máxima del nido, y la distancia entre éste y el nido conespecífico activo más cercano, estuvieron significativamente relacionados con el riesgo de parasitismo. Sólo la radiación fotosintéticamente activa explica el 65% de la variación del riesgo de parasitismo en el modelo final. A pesar de que los niveles de radiación solar que llegan a los nidos son muy bajos (<4% de radiación UV-B y UV-A, 5% de PAR, y 22% de PAR e IR en días despejados), los niveles de UV-B, UV-A, y radiación visible e IR fueron significativamente más bajos en los nidos no parasitados. Estos resultados aportan la primera evidencia de la relación entre el riesgo de parasitismo y el ocultamiento del nido en relación al ambiente lumínico del microhabitat del nido, con los nidos más iluminados sufriendo una tasa de parasitismo mayor.

BROOD PARASITISM CAN be considered a strong selective force, given that brood parasites can reduce a host's reproductive success. If a host recognizes the parasite egg, it may renest and incur a further reproductive cost; but if a host is fooled by the parasite, the host's whole reproductive output for the season can be lost (Rothstein 1990). The interaction between brood parasites and hosts can give rise to the evolution of host defense mechanisms for avoiding parasitism (Rothstein 1975), as well as more sophisticated techniques by the parasite to counteract them (Davies and Brooke 1989a, b). Dawkins and Krebs (1979) termed this coevolutionary cycle an "arms race," in which each party responds to selection pressure imposed by the other by way of adaptations and counteradaptations.

Studies of coevolution between parasites and hosts have mainly focused on antiparasitism defenses used by hosts to avoid the costs of brood parasitism. These defenses can be classified as occurring before parasitism ("preparasitism defenses") or after parasitism has taken place ("postparasitism defenses"). Among the best-studied preparasitism defenses are those related to the risk of parasitism with nest-site selection by the host, based on reducing the potential capacity of the parasite to detect a host nest. Two hypotheses have been proposed in relation to preparasitism defenses: (1) the "nest-exposure" hypothesis (Burhans 1997, Clotfelter 1998, Moskát and Honza 2000, Clarke et al. 2001), which suggests that visually conspicuous nests are at higher risk of parasitism, and (2) the "perch-proximity" hypothesis (Alvarez 1993, Øien et al. 1996, Clotfelter 1998, Moskát

and Honza 2000), which predicts that nests in proximity to parasite vantage points (e.g., trees) may suffer a higher frequency of parasitism.

Studies based on the first hypothesis have estimated visibility and concealment of the nests from the point of view of a researcher, but have not used objective and repeatable methods (Clotfelter 1998, McLaren and Sealy 2003). Visibility and concealment of nests have always been difficult variables to measure. Previous studies have suggested that vegetation structure surrounding the nest may play an important role in parasitism risk, with dense and closed canopies surrounding a nest decreasing levels of brood parasitism (Brittingham and Temple 1996). However, approaches comparing vegetation structure have only considered vegetation features on a broad scale (~100 m around a nest; Brittingham and Temple 1996, Larison et al. 1998), even though vegetation features in the immediate nest microhabitat are likely to influence parasitism risk.

Most postparasitism defenses are based on recognition of the parasitic egg, leading to egg ejection or nest desertion (e.g., Davies 2000). A parasite can counteract this antiparasitism defense by laying mimetic eggs. Although some instances of near-perfect mimicry have been observed, most studies on egg colors have shown visual differences between host and parasite eggs in spot pattern and coloration (Lotem et al. 1995, Øien et al. 1995, Lahti and Lahti 2002), including in the ultraviolet (UV) range (Cherry and Bennett 2001). These differences may increase egg recognition and host rejection if illumination within the nest is sufficient (Langmore et al. 2005). Recent studies

using spectrophotometers have shown that coloration differences are restricted to wavelength ranges (Cherry and Bennett 2001, Avilés et al. 2004) that may be invisible to human eyes. Because egg recognition takes place in the host nest, microhabitat light conditions may influence the effectiveness of potential distinguishing signals (Endler 1992, 1993). Lack of certain wavelengths, such as UV radiation, or decreased irradiance attributable to filtering by vegetation or to weather conditions, may lead to failure in egg discrimination, as suggested by Cherry and Bennett (2001) in the "light environment" hypothesis. Thus, nest light environment, in terms of both quantity and quality of light, may play an important role in any arms race between host and parasite (Cherry and Bennett 2001, Langmore et al. 2005). However, no attempt has been made to objectively test the importance of nest light environment on preparasitism defenses.

We examined whether the light environment in the microhabitat of the nest, as well as other nest-structure characteristics related to visual cues, affect the potential risk of parasitism by Common Cuckoo (*Cuculus canorus*; hereafter "cuckoo") on Great Reed Warblers (*Acrocephalus arundinaceus*). We tested the hypothesis that the quantity and quality of light getting into the nest play a role in the tradeoff between pre- and postparasitism defenses.

METHODS

The study was conducted in the Nobeyama highlands (35°57'N, 138°28'E), Nagano prefecture, central Japan, during May–July 2004. The study site is on a plateau with an average elevation of 1,350 m above sea level and is ~120 km south of the city of Nagano. In this area, reed beds occur mainly in small patches among wooded vegetation, composed primarily of maple trees (*Acer ginnala*) and willow bushes (*Salix integra*), and also on both sides of small streams (1–2 m wide). Host nests were searched for systematically during the breeding season. The earliest clutches were initiated toward the end of May, and laying continued until the end of July. Only nests with at least one host or cuckoo egg were considered in the final analysis ($n = 57$ nests). All nests were found during nest building or egg laying. To detect cuckoo parasitism, nests were checked daily during

egg laying and on the day of clutch completion. Eggs were numbered with a felt-tip marker to indicate their position in the laying sequence. Parasitized nests were also checked daily during the first six days after parasitism or until rejection took place, in accordance with Lotem et al. (1995). Nests in which cuckoo eggs were accepted were checked until hatching to detect possible late rejections and predation. The frequency distribution of cuckoo parasitism over the breeding season was analyzed by dividing the breeding season into two-week intervals. For each interval, the percentage of parasitized nests in relation to nests potentially available during this period was estimated.

In situ nest light environment and nest situation and structure were measured in all nests at the laying stage of the host, regardless of whether they were parasitized. We used 17 independent variables (Table 1), chosen on the basis of their potential predictive power. To characterize the light environment of each nest, solar-radiation measurements were taken from 1100 to 1300 hours on cloudless days, to obtain the maximum potential radiation levels in nests. Light environment was characterized according to the absolute solar-radiation values within the nest and the percentage of solar radiation in the nest compared with unobstructed full solar radiation measured at the same time on the same site and at the height of the nest. The UV-B radiation (280–315 nm; Commission Internationale de L'Eclairage definition) and UV-A radiation (315–400 nm) (Wm^{-2}) were measured using the radiometer RM-12 (Dr. Gröbel UV-Elektronik, Ettlingen, Germany) together with UV-B and UV-A radiation sensors from the same company. Solar radiation from 400 nm was measured using a LI-250 light meter (LI-COR, Lincoln, Nebraska) together with compatible Li-COR radiation sensors: a quantum sensor to measure photosynthetically active radiation (PAR) (400–700 nm; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and a pyranometer sensor to measure PAR plus infrared (IR) radiation (400–1,100 nm; Wm^{-2}). Fifteen light measurements were performed in each nest, and the mean value was used for each model. All sensors were set at right angles to the ground when measuring.

To predict the potential risk of parasitism on Great Reed Warbler nests in relation to their light environment, a stepwise logistic regression of parasitism on the selected variables was performed. This technique has been shown to

TABLE 1. Nest environmental variables used to model the potential risk of Common Cuckoo parasitism in the Great Reed Warbler, and their hypothesized effects on the risk of cuckoo parasitism (+ = direct relationship, - = inverse relationship).

Code	Variable	Hypothesized effect
<i>dNests</i>	Distance between nest and nearest active conspecific neighbor (m)	+
<i>dEdge</i>	Minimum distance from nest to edge of the reeds (cm)	-
<i>dPerch</i>	Horizontal distance from nest to the closest perch site (tree or wire) for cuckoos (m)	-
<i>Height</i>	Height of nest above ground level, measured to bottom of nest (cm)	+
<i>Veget</i>	Height of vegetation above nest, measured from top of nest (cm)	-
<i>Visib</i>	Nest visibility by observer (measured on a five-state relative scale)	+
<i>NestH</i>	Nest cup height (cm)	+
<i>NestW</i>	Maximum nest width (cm)	+
<i>Nestw</i>	Minimum nest width (cm)	+
<i>UVBin</i>	UVB radiation (280–315 nm) in the nest	+
<i>RelUVB</i>	Percentage of UVB radiation in the nest	+
<i>UVAin</i>	UVA radiation (315–400 nm) in the nest	+
<i>RelUVA</i>	Percentage of UVA radiation in the nest	+
<i>PARin</i>	PAR radiation (400–700 nm) in the nest	+
<i>RelPAR</i>	Percentage of PAR radiation in the nest	+
<i>PAR+IRin</i>	PAR+IR radiation (400–1,100 nm) in the nest	+
<i>RelPAR+IR</i>	Percentage of PAR+IR radiation in the nest	+

be a powerful analytical tool, capable of analyzing the effects of one or several independent variables, discrete or continuous, over a dichotomous variable (Hosmer and Lemeshow 1989). We assessed the classification accuracy of the model with regard to its sensitivity, specificity, and correct classification rate. We assessed the strength of the agreement between the model and the parasitism data with Cohen's kappa (κ ; Fielding and Bell 1997).

Multicollinearity among predictive variables may complicate explanations, because the effects of positively correlated variables may be difficult to distinguish and negatively correlated variables may obscure one another (Borcard et al. 1992, Legendre 1993). To account for collinearity between variables in the model, we performed a variation-partitioning procedure. This allowed us to specify how much variation in the final model was explained by the pure effect of each variable (R_{pi}^2), by the collinearity with other variables in the model, or by their shared effect (Legendre 1993, Legendre and Legendre 1998). The amount of variation in the final model that was explained by each variable (R_i^2), both alone and in conjunction with other variables, was obtained by using the squared value of the Pearson correlation coefficient between the values obtained in the final

model and in a model based only on the variable. The pure effect of each variable (R_{pi}^2) was assessed by subtracting the variation explained by the other variables combined from the variation explained by the explanatory model. The combined effect of two variables may be obtained by subtracting their pure effects from their combined effect ($R_{i+j}^2 - [R_{pi}^2 + R_{pj}^2]$). Differences between media were tested by *t*-tests ($P > 0.05$).

RESULTS

CUCKOO PARASITISM

The frequency of cuckoo parasitism was 39% (22 out of 57 nests). All parasitized nests received only one cuckoo egg, except for a single nest that was parasitized twice at the end of the breeding season, with the second egg laid after the ejection of the first one. One empty nest and one incubated clutch were found parasitized. Ten out of 22 (45%) parasitic eggs were accepted by the hosts. Rejection responses were observed in 41% of parasitized nests, with ejection observed in 7 of 9 nests and desertion in 2 of 9 nests. Two parasitized nests were depredated before we could confirm the acceptance or rejection of the parasitic egg. Total predation rate on Great Reed

Warbler nests was 16%. The frequency of parasitism through the study period was not constant; it increased from 27% in the first two weeks to 75% at the end of the period (Fig. 1).

THE MODEL

The model included three variables: percentage of PAR+IR radiation (400–1,100 nm) in the nest, distance between the nest and the nearest active conspecific neighbor, and maximum nest width (Table 2). These results are in concordance with the hypothesized effects of these variables (i.e., parasitism risk increased with increasing *RelPAR+IR*, *dNests* and *NestW*; Table 1). The sensitivity of this model was 68.8%, the specificity 92.3%, the correct classification rate 84.1%, and the κ value 0.642. Following Altman (1991), the strength of agreement of our model is classified as good ($0.6 < \kappa < 0.8$).

The results of variation partitioning are shown in Figure 2. The percentage of PAR+IR radiation reaching the nest explained most variation (65%) in the model. Maximum nest width explained 23% of the remaining variation, whereas distance to conspecific nests accounted for a small proportion (16%) of variation in the model. About 12% of variation was explained simultaneously by solar radiation getting into the nest and by nest width, independently of the degree of isolation of the nest. The interaction

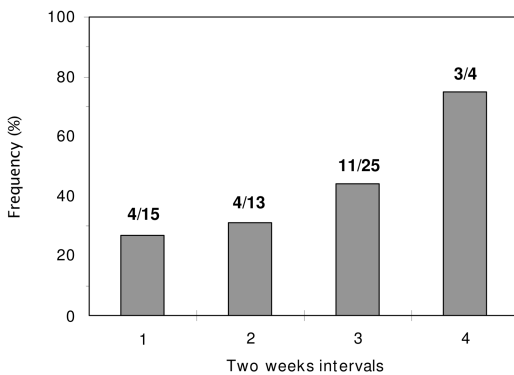


FIG. 1. Frequency distribution (%) of Common Cuckoo parasitism during the present study, in two-week intervals: (1) 26 May to 8 June, (2) 9–22 June, (3) 23 June to 6 July, and (4) 7–20 July. Values over bars show the number of parasitized nests versus the total number of nests available for parasitism during the period.

between distance to the nearest conspecific nest with the other variables was negative.

LIGHT ENVIRONMENT IN THE NESTS

With no vegetative canopy filtering solar radiation, UV-B and UV-A, PAR, and PAR plus IR radiation mean values were $1.43 \pm 0.20 \text{ Wm}^{-2}$, $38.34 \pm 2.81 \text{ Wm}^{-2}$, $2,014.3 \pm 103.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$, and $1,093.5 \pm 81.2 \text{ Wm}^{-2}$, respectively. However, solar radiation levels in the nest were very low compared with full solar radiation: $1.2 \pm 1.3\%$ UV-B, $2.0 \pm 1.7\%$ UV-A, $2.5 \pm 2.0\%$ PAR and

TABLE 2. Variables included in the model and their coefficients (β), standard errors (SE), Wald test values (Wald 1943), and significance (*P*). Variables are ranked according to their order of entry into the model and coded as in Table 1.

Variable	β	SE	Wald	<i>P</i>
<i>RelPAR+IR</i>	0.355	0.120	8.701	0.0032
<i>dNests</i>	0.140	0.068	4.259	0.0390
<i>NestW</i>	0.129	0.063	4.215	0.0040
Constant	-20.898	8.197	6.499	0.0108

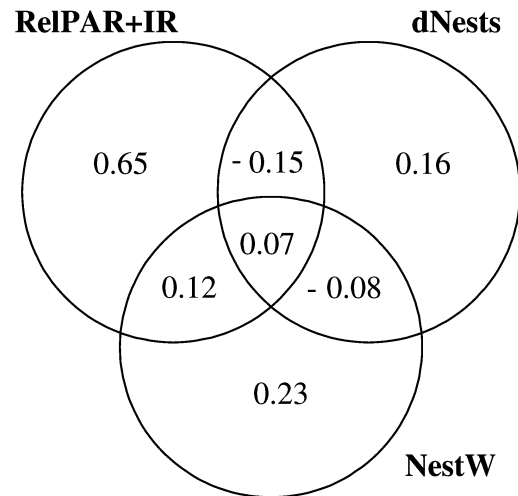


FIG. 2. Results of variation partitioning in the model. Values shown in the diagrams are percentages of variation explained exclusively by percentage of PAR+IR radiation (400–1,100 nm) that reaches the nest (*RelPAR+IR*), by distance between nest and the nearest active conspecific neighbor (*dNests*), by maximum nest width (*NestW*), and by the interactions between these variables.

15.9 ± 5.8% PAR plus IR. In fact, no UV-B and UV-A radiation were found in 37% and 10% of the nests, respectively, and <1% of solar radiation penetrated 49% of the nests for UV-B radiation and 33% for UV-A radiation. Despite these low solar-radiation levels in the nests, significant differences were observed between nonparasitized and parasitized nests in UV-B and UV-A radiation and PAR plus IR radiation (Fig. 3). Solar radiation levels in these wavelengths were between 30% and 50% lower in nonparasitized nests than in parasitized ones.

DISCUSSION

The risk of cuckoo parasitism of Great Reed Warbler nests was reasonably well predicted by a limited number of variables describing the light environment and placement of the nest. Although good model fit does not necessarily imply a correct inference of causation (James and McCulloch 1990), our model suggests that the highest risk of parasitism is found in exposed and bigger nests and in nests located away from breeding territories of other conspecifics.

The first variable in the model, and the most important one, percentage of PAR plus IR radiation reaching the nest, was highly related to the vegetation canopy over the nest. The vegetation canopy included both the photosynthetic and nonphotosynthetic parts of the plants (irradiance and heat absorption). The percentage of PAR plus IR radiation reaching the nest, together with maximum nest width,

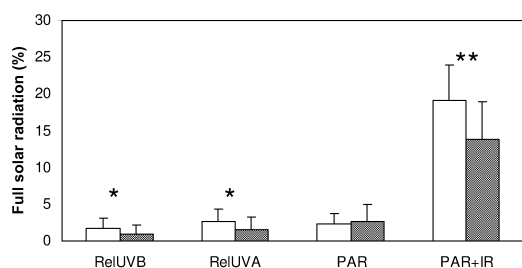


FIG. 3. Percentages of UVB, UVA, PAR, and PAR+IR, compared with full solar radiation, in parasitized (white bars) and nonparasitized nests (dark bars). Data are shown as means ± SD ($n = 22$ for parasitized nests; $n = 35$ for nonparasitized nests; * = significantly different at $P < 0.05$; ** = significantly different at $P < 0.01$).

explained 88% of variation in the model, and both variables together may be identified as nest exposure and visibility. These results are in agreement with the nest-exposure hypothesis (Clotfelter 1998), which predicts that nests more visible to brood parasites are more likely to be parasitized. This hypothesis has been supported by other authors who found that nest concealment and visibility were important factors in assessing the parasitism risk of different species (Brittingham and Temple 1996, Burhans 1997, Clarke et al. 2001), including an earlier study of the Great Reed Warbler (Moskát and Honza 2000). Nevertheless, in all these studies, concealment and visibility of nests were estimated using a subjective score from the perspective of the cuckoo or as nest visibility by the observer. In the present study, the light environment in the nest was used, for the first time, to measure nest exposure in a quantitative and objective way. Our results confirm the link between conspicuousness-related nest characteristics and the risk of cuckoo parasitism in Great Reed Warblers.

Contrary to previous studies (Alvarez 1993, Øien et al. 1996, Moskát and Honza 2000), the distance from a cuckoo's vantage point to a host's nest was not an important variable predicting parasitism risk. This may be attributable to the very patchy structure of reed beds; the distance between potential cuckoo perch sites and Great Reed Warbler nests was always short (<7 m). In such a patchy habitat, the maximum distance from a nest to the closest potential perch is probably sufficient to allow a parasite to detect the host's breeding activities.

The other variable entering in the predictive model, explaining 16% of the variation, was distance between the nest and the nearest active conspecific neighbor. This result suggests the importance of reducing internest distances by Great Reed Warblers to reduce the risk of cuckoo parasitism. The explanation for this may be the same one proposed by Øien et al. (1996) in a closely related species, the Reed Warbler (*A. scirpaceus*). These authors suggested that the close vicinity of another active pair may increase the possibility of a host detecting a cuckoo's presence and attacking it more effectively than would a solitary breeding pair. Furthermore, because a Great Reed Warbler is ~2.5× heavier than a Reed Warbler (Cramp 1992), attacking a cuckoo cooperatively may be a more effective

and important preparasitism defense in the former species.

Our results showed that nonparasitized nests received significantly lower UV and visible plus IR radiation than parasitized nests, which is in agreement with the predictive model. The reduced success of cuckoos in locating a nest on a dark site may give a selective advantage, through decreased parasitism risk, to hosts that avoid nests with brighter environments. These results are in concordance with the "nest-site constraint" hypothesis (Grim 2002), which suggests that selection of safe nest sites may follow age-dependent patterns, with experienced breeders selecting higher-quality sites for nesting (e.g., Sæther 1990). Lotem et al. (1992) found, in a Great Reed Warbler population close to our study area (100 km), that adults arrived earlier and were less tolerant of cuckoo eggs than later-arriving juveniles. In our study population, parasitism rate increased over the breeding period and, though the birds' ages were unknown, if experienced individuals arrived earlier and chose higher-quality nest sites, that may have reduced their parasitism risk. Thus, selection should favor host consideration of the quality of nest sites, because this may reduce brood parasitism or predation risk. This was suggested by Øien et al. (1996), who found that nests away from trees were less parasitized than those built near trees. These authors suggested that hosts identified "low-risk areas" as better habitats, and these sites were occupied by higher-quality individuals. The results of our study suggest that breeders may identify a high-quality habitat for nesting as one that receives low solar radiation levels, and this raises the question of how brood parasitism can influence the evolution of host nest-site selection.

All nests in our study received relatively low solar irradiance levels. Nevertheless, nonparasitized nests received significantly less irradiance than parasitized nests. Nesting in more concealed places, where less solar radiation reached the nest, may be a preparasitism defense. However, hosts may have to face an important tradeoff between pre- and postparasitism defenses when choosing well-concealed nests: though hidden and darker nests may prevent parasitism, these conditions also may make recognition and rejection of parasite eggs difficult once parasitism has

occurred. Furthermore, this compromise may include a thermoregulatory cost, given that it may be more energetically expensive to keep eggs warm in a shady nest than in a brighter one. For example, Langmore et al. (2005) measured visible light in different host nests and reported higher rejection rates in lighter nests than in darker ones. Ultraviolet radiation may play an important role in egg rejection as well. The discovery that birds are sensitive to UV light has led to studies unmasking visual differences of eggs imperceptible to humans (Bennett and Cuthill 1994, Cherry and Bennett 2001, Langmore et al. 2003, Avilés et al. 2004). These studies have explained, in some cases, why nonmimetic eggs are sometimes accepted by the host. However, all these studies used artificial light sources that did not simulate natural illumination, requiring *in situ* extrapolations to verify their potential relevance with regard to real nests. In the present study, we found that light environment in the nest was quantitatively and qualitatively different from that of full solar radiation because of concealing vegetation. Quantitative changes in light environment in the nest may affect the perception of achromatic egg differences such as brightness, as observed by Cherry and Bennett (2001), whereas qualitative changes may affect chromatic differences, as observed by Lahti and Lahti (2002). Although, in general, achromatic bird vision is more light-sensitive than chromatic vision (Bowmaker et al. 1997, Hart et al. 2000), the evolution of achromatic or chromatic visual skills in host species could depend on the light environment in the nest. However, to our knowledge, no study has tested the relationships among egg coloration differences, light quality in the nest, and rejection rates. Such a future study could reveal a new level of complexity in the host-parasite arms race.

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