



Does clutch variability differ between populations of cuckoo hosts in relation to the rate of parasitism?

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To aid discrimination of mimetic cuckoo eggs, hosts of avian brood parasites would theoretically benefit by laying clutches that are more uniform in appearance and by laying clutches that differ from those of other females in the population. Support for these hypotheses is equivocal, particularly amongst studies that have utilized reflectance spectrophotometry; quantitative studies comparing clutch variation between parasitized and unparasitized host populations have supported these hypotheses, whereas experimental studies comparing clutch variation between rejector and acceptor individuals within a population generally have not. Here we extend the approach of comparing population differences in clutch variation by asking whether parasitized populations that suffer relatively higher parasitism rates, and are therefore subject to more intense selection for host defences, show lower within-clutch variation and higher between-clutch variation than populations with low parasitism rates. We used reflectance spectrophotometry to compare clutch variation in two hosts of the pallid cuckoo, *Cuculus pallidus*, each of which exhibits two geographically distinct subspecies that differ in parasitism rates (red wattlebirds, *Anthochaera carunculata*, and yellow-throated miners, *Manorina flavigula*). A third host species, the yellow-tufted honeyeater, *Lichenostomus melanops*, was included as a control. Our results do not support either hypothesis, and are consistent with experimental studies that also failed to support the hypothesis, casting doubt on the generality of these processes.

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Obligate brood parasites lay their eggs in the nests of other birds, reducing their hosts' fitness in order to increase their own. If the host adopts stratagems to better identify and reject the foreign egg, the parasite may evolve eggs that more closely resemble the host clutch, potentially locking the host and parasite into an evolutionary arms race (Brooke & Davies 1988; Davies & Brooke 1989a, b; Langmore et al. 2003). Mimicry of host eggs by parasitic cuckoos can be remarkably accurate (e.g. Starling et al. 2006), and hosts must in turn distinguish and remove the foreign egg. This provokes the question of whether there are any further steps that hosts can take in the arms race against cuckoos. One proposed, but contentious, adaptation to facilitate the discrimination of parasitic eggs is the reduction of variation in egg appearance within host clutches (within-clutch variation) and the increase in clutch variation among hosts in a population (between-clutch variation) (Victoria 1972; Davies & Brooke 1989b; Øien et al. 1995). This theory

assumes that a foreign-looking egg is easier to pick out of a clutch of uniform-looking eggs (Davies & Brooke 1989b; Stokke et al. 1999; Kilner 2006) and high variation among clutches makes it harder for the cuckoo to mimic more than one host's clutch (Swynnerton 1918; Davies & Brooke 1989b; Honza et al. 2004; Kilner 2006).

For over 35 years numerous interspecific and intraspecific studies have investigated the way cuckoo parasitism has affected differences in eggshell appearance within and between host clutches (reviewed in Kilner 2006). However, since avian visual systems are more extensive than that of humans, and include sensitivity to ultraviolet light (the bird-visible waveband spans ca. 300–700 nm, compared to 400–700 nm for humans, Bennett & Cuthill 1994), egg appearance must be evaluated independently of human biases. Unfortunately, many investigations have relied on subjective human assessments of colour, so the results need to be interpreted with caution. Within the remaining studies (Avilés & Møller 2003; Avilés et al. 2004; Lahti 2005; Cherry et al. 2007; Poláčiková et al. 2007; Landstrom et al. 2010), much ambiguity remains over the effects of parasitism on both within-clutch variation and between-individual variability.

One of the main approaches to investigating whether brood parasitism influences clutch variability is to compare the degree of egg variability between parasitized and unparasitized populations

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of the same host species. This approach has been adopted by three studies that used quantitative assessment of egg coloration to assess within-clutch variation (computer-based image analysis: Moskát et al. 2002; spectrophotometric analysis: Avilés & Møller 2003; Lahti 2005) and two studies that assessed between-clutch variation (computer-based image analysis: Moskát et al. 2002; spectrophotometric analysis: Lahti 2005). All studies found support for the hypotheses; populations that were sympatric with cuckoos showed lower within-clutch variability and higher between-clutch variability than allopatric populations. By contrast, experimental studies that used reflectance spectrophotometry to investigate clutch variation between rejector and acceptor individuals within a population generally failed to find any support for the hypothesis (Avilés et al. 2004; Cherry et al. 2007; Landstrom et al. 2010; but see Poláčiková et al. 2007).

Here we extend the approach of comparing population differences in clutch variation by investigating whether clutch variability differs between parasitized populations of a host species in relation to the rate of parasitism, and therefore the intensity of selection, by cuckoos. We used reflectance spectrophotometry to compare clutch variation in two hosts (red wattlebirds, *Anthochaera carunculata* and yellow-throated miners, *Manorina flavigula*) of the pallid cuckoo, *Cuculus pallidus*, each of which is represented by two subspecies that suffer different rates of parasitism. We also included a third host (yellow-tufted honeyeaters, *Lichenostomus melanops*), as a control.

METHODS

Species Selection

Rates of parasitism were based on the large-scale survey conducted by Brooker & Brooker (1989), which provided over 5000 records of cuckoo parasitism for 12 individual biogeographical regions within Australia (based on Blakers et al. 1984). Three honeyeater host species were selected for analysis on the basis of their geographically variable parasitism rate by pallid cuckoos (Table 1): red wattlebirds occur in southern Australia and are major hosts in the southwest, but not in the southeast, and yellow-throated miners are prevalent across most of the country and are common hosts in the west, but are less parasitized in the east (Brooker & Brooker 1989). Although both of the chosen species have more than two geographically separated subspecies, we chose for comparison only the most and the least parasitized subspecies.

Table 1

Records of pallid cuckoo, *Cuculus pallidus*, parasitism for two geographically distinct subspecies of each host (red wattlebird, *Anthochaera carunculata*; yellow-throated miner, *Manorina flavigula*; yellow-tufted honeyeater, *Lichenostomus melanops*)

| Host subspecies | Region* | Proportion parasitized† | %Parasitism‡ | Number of clutches§ |
|---------------------------------|---------|-------------------------|--------------|---------------------|
| Red wattlebird | | | | |
| <i>carunculata</i> | SE, MD | 11/376 | 3% | 18 |
| <i>woodwardi</i> | SW | 42/139 | 30% | 19 |
| Yellow-throated miner | | | | |
| <i>flavigula</i> | SE, MD | 5/376 | 1% | 18 |
| <i>obscura</i> | SW | 17/139 | 12% | 12 |
| Yellow-tufted honeyeater | | | | |
| <i>cassidix</i> | SE, MD | 10/376 | 3% | 5 |
| <i>meltoni</i> | SE, MD | 9/376 | 3% | 20 |

* Biogeographical regions, SE (southeast), MD (Murray-Darling) and SW (southwest), from Brooker & Brooker (1989).

† Number of recorded parasitisms for each subspecies in region/total number of recorded parasitisms in region.

‡ Percentage of total regional pallid cuckoo parasitisms for each subspecies.

§ Total number of clutches measured for this study.

A third species, the yellow-tufted honeyeater, was used as a control because the two subspecies appear to experience equally low rates of parasitism (Brooker & Brooker 1989). None of these hosts are listed as major hosts of any other species of cuckoo (Brooker & Brooker 1989), although in the eastern ranges north of Sydney, red wattlebirds are parasitized by the larger Australian koel, *Eudynamis scolopacea* (Brooker & Brooker 1989; Davies 2000). Because of this parasitism by a different species of cuckoo, and the potential for conflicting selection pressures on egg colour, red wattlebird clutches from Queensland were excluded from the analyses.

The relative rate of parasitism for each population was estimated by dividing the number of records of parasitism by pallid cuckoos for each population by the total number of records of parasitism for all species in their respective biogeographical region (Table 1). Both subspecies of yellow-tufted honeyeater are located within the same region, so the number of recorded parasitism events for each population was determined by using localities provided by the *Australian Cuckoo-Host Database* (Brooker & Brooker 2005) and assigning subspecies to the clutches based on known subspecies distribution within the region. We confirmed for each species that higher numbers of records of parasitism in a given population were not simply a consequence of higher host density. For each subspecies, we used the *Atlas of Australian Birds* (Barrett et al. 2003) to calculate the total number of 1-degree cells within the biogeographical zones identified in Brooker & Brooker (1989) in which the subspecies occurred at >40%, >30%, >20%, >10% and >0% reporting rates. We then compared these data between the two subspecies of each species using a contingency table analysis. Although the red wattlebird and the yellow-throated miner are major hosts of pallid cuckoos in the southwest, both were more widespread in the southeast than in the southwest, and neither showed a significant difference in density between the two regions (red wattlebird: $\chi^2_4 = 7.87$, $P = 0.096$; yellow-throated miner: $\chi^2_3 = 5.96$, $P = 0.11$). Similarly, *Lichenostomus melanops cassidix* has a smaller distribution but a similar density to the comparison subspecies, *Lichenostomus melanops meltoni* (Fisher's exact test: $P = 1$).

Clutch Measurements

Egg clutches used for colour analysis were provided by CSIRO's Australian National Wildlife Collection, Canberra, the Australian Museum Oological Collection, Sydney, and the Department of Terrestrial Vertebrates, Western Australian Museum, Perth. We used information from the museum databases to determine clutch locality and the date that each clutch was collected. We included only complete clutches with clear labelling and collection dates provided. Also, clutches that contained either dirty or heavily cracked eggs were excluded, since these conditions may give inaccurate reflectance readings. Sample sizes are provided in Table 1.

Eggshell colour was measured using a USB2000 reflectance spectrophotometer (OOIBASE software by Ocean Optics), following the methods described in Landstrom et al. (2010). Reflectance was taken over the range of bird-visible wavelengths (300–700 nm). Four readings were taken in two regions on each egg, the 'side' and the 'ring', for a total of eight measurements. The 'side' corresponds to the background colour (usually measured from the middle of the egg), and the 'ring' refers to a region of dense speckling or darker coloration that usually appears near the base of maculated eggs.

Statistical Analysis

We used principal component analyses (PCA) in all statistical investigations. PCA summarizes the most important variation in

multidimensional data sets for analysis and as such is useful for evaluating variation in spectral data. For each species, the mean reflectance spectra for each egg was entered into two separate principal components analyses (one for ring measurements, the other for side measurements) and the first three principal components were determined in each case using GenStat v.10 (Payne et al. 2007). Both subspecies were included in the same analysis for each species.

Are there differences in clutch variation between subspecies?

To examine possible differences between subspecies in the amount of between-clutch and within-clutch variation in egg appearance, we followed the statistical methods of Landstrom et al. (2010). For each species, the six PCs (PC1, PC2 and PC3 for both ring and side measurements) were entered separately into generalized linear models. To account for having multiple eggs in a clutch, we identified each egg separately within each clutch and gave each clutch a separate nest identifier. We also included subspecies in the models, and we controlled for the age of the eggs in the models by including the date of collection, although age did not have a significant effect. The resulting accumulated analysis of variance yielded the amount of variance associated with within-clutch and between-clutch variation, and variance ratios (F statistics) were generated for all comparisons of interest. The species predicted to have more variability was set as the numerator, and that predicted to have less variability was set as the denominator of the variance ratio. For the control species, the ratio was arbitrarily placed so that either subspecies was predicted to have 'less within-clutch' and 'more between-clutch' variation than the other. Significance in either direction was tested.

RESULTS

The mean reflectance spectrum for the two subspecies of each species was plotted for ring and side measurements (Fig. 1). The first three principal components together explained 98.4–99.6% of the total variance in spectrum shape for the side (mean \pm SE, $N = 3$: PC1: $86.2 \pm 0.6\%$; PC2: $8.5 \pm 0.6\%$; PC3: $4.4 \pm 0.6\%$) and the ring (PC1: $89.0 \pm 1.4\%$; PC2: $6.1 \pm 1.3\%$; PC3: $4.1 \pm 0.06\%$) of each species. Plots of the three principal component coefficients illustrate major sources of variation in the spectra they represent (Fig. 2).

Does Rate of Parasitism Affect Within-clutch Variation?

Next, we examined whether the variation within clutches was lower in the more parasitized populations. Of six variables tested (PC1, PC2, PC3 for ring and side) for both of the species with contrasting parasitism rates between populations (red wattlebirds and yellow-throated miners), none differed significantly in the predicted direction (Table 2; corrected experimentwise significance level for six comparisons: critical $P = 0.0085$; Dunn–Sidak method; Sokal & Rohlf 1995). Nor were there any significant differences between the two subspecies of the control species (Table 2).

Does Rate of Parasitism Influence Between-clutch Variation?

Finally, we tested whether populations with greater rates of parasitism have more between-individual variation. Again, there were no significant differences between subspecies (Table 3; corrected experimentwise significance level for six comparisons: critical $P = 0.0085$; Dunn–Sidak method; Sokal & Rohlf 1995). Nor were there any significant differences between the two subspecies of the control species (Table 3).

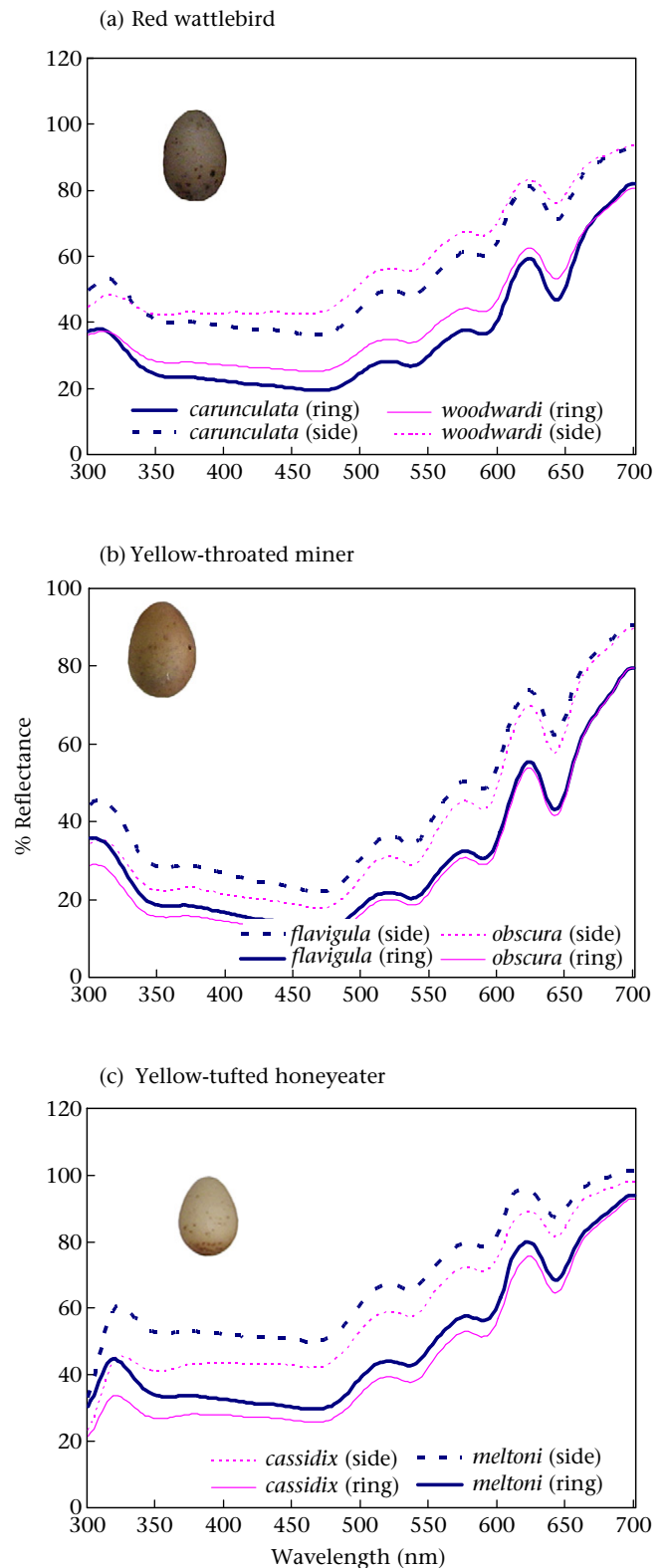


Figure 1. Mean reflectance spectrum of ring and side regions of eggs for two subspecies of red wattlebirds, *Anthochaera carunculata*, yellow-throated miners, *Manorina flavigula*, and yellow-tufted honeyeaters, *Lichenostomus melanops*. An example of each species' egg is shown in the upper left-hand corner of each panel. Dashed lines = side measurements; solid lines = ring measurements; thin pink lines = more heavily parasitized subspecies (a, b). Species are listed in putative order of parasitism disparity, from red wattlebirds (highest) to yellow-tufted honeyeaters (little/none); (a) *A. c. woodwardi* ($N = 41$), *A. c. carunculata* ($N = 37$); (b) *M. f. obscura* ($N = 42$), *M. f. flavigula* ($N = 57$); (c) *L. m. cassidix* ($N = 10$), *L. m. meltoni* ($N = 41$).

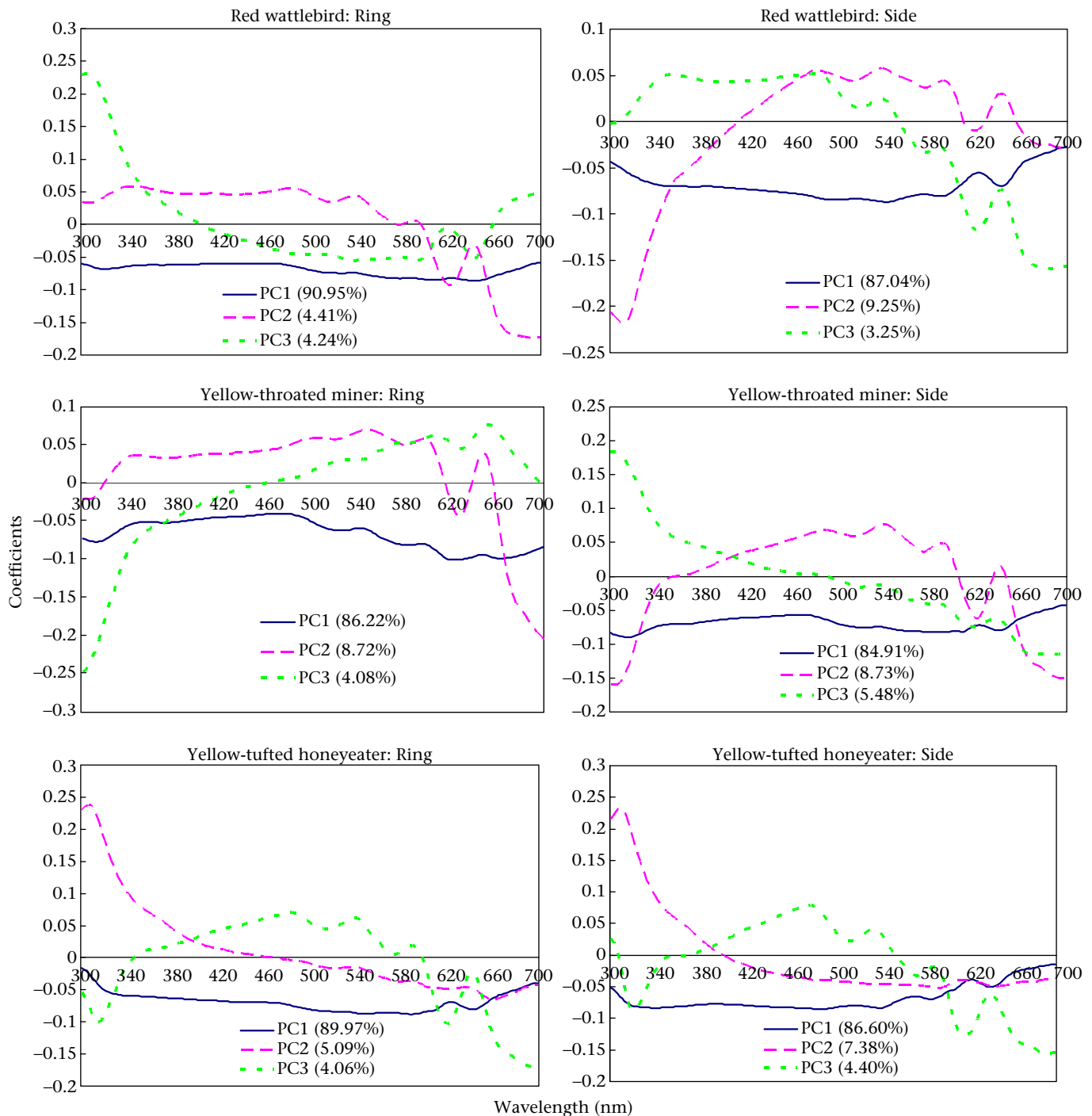


Figure 2. Coefficients of PC1, PC2 and PC3 against wavelength measurements for ring and side regions of eggs from two subspecies of red wattlebirds, *Anthochaera carunculata*, yellow-throated miners, *Manorina flavigula*, and yellow-tufted honeyeaters, *Lichenostomus melanops*. Percentage of variation explained by each PC is given in parentheses.

DISCUSSION

Our results failed to support the hypotheses that hosts in relatively more parasitized populations lay clutches of eggs that are more uniformly similar in appearance, or that they are more likely to lay eggs that differ from those of other females in the population. However, differences in parasitism rates between populations of pallid cuckoo hosts might arguably have had a modest influence on within-clutch egg variability; in both host species the more heavily parasitized subspecies showed a tendency towards reduced within-

clutch variation, whereas this was not the case for the control species (Table 2). By contrast, differences in between-clutch variation showed no evidence of a directional effect.

One possible explanation for these nonsignificant results is that parasitism rates of different populations may vary over time, such that populations with currently low rates of parasitism may have been parasitized heavily in the past. This could result in high between-clutch variation and low within-clutch variation persisting despite reduced parasitism, if clutch modification does not carry a cost (Rothstein 2001).

Table 2

Difference in within-clutch variation between subspecies parasitized by pallid cuckoos based on the first three principal components for ring and side colour measurements of eggs

| Host species | | Ring | | Side | |
|--|-----|------|-------|------|-------|
| | | F | P | F | P |
| Red wattlebird N=32 clutches, 66 eggs df=21, 13 | PC1 | 0.49 | 0.930 | 0.47 | 0.941 |
| | PC2 | 0.82 | 0.667 | 0.65 | 0.817 |
| | PC3 | 2.69 | 0.035 | 0.60 | 0.853 |
| Yellow-throated miner N=30 clutches, 99 eggs df=42, 27 | PC1 | 1.78 | 0.058 | 1.93 | 0.037 |
| | PC2 | 1.10 | 0.400 | 1.00 | 0.508 |
| | PC3 | 1.06 | 0.441 | 1.08 | 0.422 |
| Yellow-tufted honeyeater N=25 clutches, 51 eggs df=22, 4 | PC1 | 1.02 | 0.561 | 0.51 | 0.866 |
| | PC2 | 0.44 | 0.907 | 0.14 | 0.999 |
| | PC3 | 0.24 | 0.989 | 0.66 | 0.765 |

Species are listed in putative order of parasitism disparity, from red wattlebirds (highest) to yellow-tufted honeyeaters (little/none). Following application of a Dunn–Sidak correction (Sokal & Rohlf 1995) for multiple comparisons, there were no significant differences between subspecies (critical $P = 0.0085$).

A further explanation may lie in the fact that all the subspecies are parasitized, but to varying degrees. Even uncommon parasitism provides some selective pressure for hosts to develop defensive abilities, particularly since the outcome of successful parasitism is so devastating to a host's reproductive fitness (Langmore et al. 2005). Consequently, heavily parasitized and occasionally parasitized populations both experience selection in the same direction, and differences in the intensity of selection between subspecies may be insufficient to cause a detectable difference in clutch variation.

Although our results differ from those comparing host populations that are sympatric versus allopatric with cuckoos (Moskát et al. 2002; Avilés & Møller 2003; Lahti 2005), they are more consistent with several experimental studies that used reflectance spectrophotometry to compare clutch variation between rejector and acceptor individuals within a population (Avilés et al. 2004; Cherry et al. 2007; Landstrom et al. 2010). In a field study involving three pallid cuckoo hosts, Landstrom et al. (2010) not only found that lower within-clutch variation does not appear to improve a host's ability to reject a foreign egg, but they also found little support for the hypothesis that higher parasitism rates select for reduced within-clutch variation. Two other studies failed to find support for the prediction that rejector individuals lay significantly less variable clutches than acceptor individuals; instead they found significantly greater within-clutch variation in rejectors (Avilés et al. 2004; Cherry et al. 2007). Taken together, these results suggest either that cuckoo parasitism exerts only moderate

Table 3

Difference in between-clutch variation between subspecies parasitized by pallid cuckoos based on the first three principal components for ring and side colour measurements of eggs

| Host species | | Ring | | Side | |
|--|-----|------|-------|------|-------|
| | | F | P | F | P |
| Red wattlebird N=32 clutches, 66 eggs df=12, 17 | PC1 | 2.15 | 0.073 | 2.11 | 0.078 |
| | PC2 | 0.4 | 0.946 | 0.48 | 0.901 |
| | PC3 | 0.73 | 0.708 | 0.8 | 0.649 |
| Yellow-throated miner N=30 clutches, 99 eggs df=10, 17 | PC1 | 0.44 | 0.907 | 1.03 | 0.461 |
| | PC2 | 2.46 | 0.049 | 0.8 | 0.627 |
| | PC3 | 1.49 | 0.226 | 0.51 | 0.863 |
| Yellow-tufted honeyeater N=25 clutches, 51 eggs df=3, 19 | PC1 | 1.07 | 0.385 | 0.28 | 0.842 |
| | PC2 | 0.24 | 0.866 | 0.17 | 0.915 |
| | PC3 | 0.61 | 0.615 | 0.15 | 0.931 |

Species are listed in putative order of parasitism disparity, from red wattlebirds (highest) to yellow-tufted honeyeaters (little/none). There were no significant differences between subspecies (critical $P = 0.0085$).

selective pressure on host clutch variability, or that selection by cuckoos is constrained by selection for other attributes of egg coloration, such as crypsis (Kilner 2006), signalling of female quality (Moreno & Osorno 2003), or use of pigmentation to strengthen the eggshell (Gosler et al. 2005).

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