Male spotted bowerbirds propagate fruit for use in their sexual display

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Cultivation may be described as a process of co-evolution and niche construction, with two species developing a mutualistic relationship through association, leading to coordinated change [1]. Cultivation is rare but taxonomically widespread, benefiting the cultivator, usually through increased access to food, and the cultivar, by improved growth and protection, driving co-evolutionary changes (Supplemental information). Humans cultivate more than food, producing clothing, construction materials, fuel, drugs, and ornaments. A population of male spotted bowerbirds *Ptilonorhynchus* (*Chlamydera*) *maculata* uses fruits of *Solanum ellipticum* (Figure 1A), not as food but as important components of their sexual display [2,3]. Here, we show that males indirectly cultivate plants bearing these fruit — the first example of cultivation of a non-food item by a species other than humans. Plants appear at bowers following male occupation (Figure 1B). Males benefit, exhibiting more fruit at their bowers. Plants benefit because fruit are deposited in better germination sites. Fruits from plants near bowers differ visually from those far from bowers, and look more similar to fruits that are preferred by males in choice tests.

Male bowerbirds at Taunton National Park, Central Queensland, do not select bower locations that already have especially high numbers of *Solanum* plants, but rather, high numbers of these plants result from local occupancy by the owner and the germination of discarded fruit near the bower. When males arrived at new, previously unoccupied sites to construct bowers, the numbers of *Solanum* plants found there were no higher than found at random sites ($p = 0.48$; Figure 1A). However, at established bowers, occupied for longer than one year, we observed more *Solanum* plants than at random sites ($p = 0.036$; Figure 1C). Male spotted bowerbirds can occupy the same bower for up to 10 years, separated by about 1 km from their neighbours, and most remain at, or very close to (< 10 m), their previous year's bower site, with only a few establishing new bower sites or moving further away each year [4]. This provides an incentive for sedentary males to cultivate an accessible source of these fruit to supply their displays in subsequent years.

Males benefit from a local supply of these fruit in two ways. First, bowers surrounded by more *Solanum* plants contained higher numbers of fruit ($r_s = 0.51$, $n = 34$, $p = 0.002$; Supplemental information). Males with many fruit also had high mating success [2]. They preferentially chose *Solanum* fruit from decoration caches, placed them disproportionately in the centre of their bower avenue, and selectively held them in their bills during displays [3]. Second, males gained a long-term fruit supply as bowers with many fruit on them in one year were

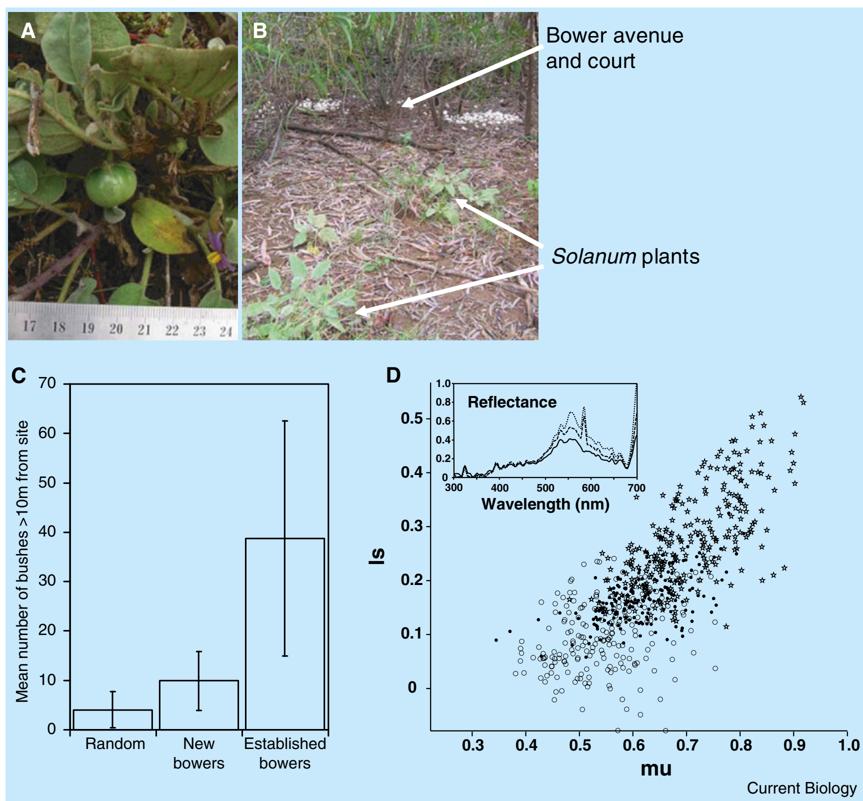

Figure 1. Fruits propagated by bowerbirds.
(A) *Solanum ellipticum* plant and fruit. Scale in cm. (B) Established bower surrounded by *Solanum* plants. (C) Mean (±1 s.e.) numbers of *Solanum* plants in 2010 at: randomly selected sites within the study area ($n = 20$); new bower sites that were being used for the first time ($n = 11$); established bower sites that had been used for more than one year ($n = 14$). (D) Visual properties of *Solanum* fruit. The inset shows mean reflectance spectra, and the main panel shows all fruits as points in avian V-type LMSU colour space. Circles and solid line: fruits collected on bowers; solid dots and broken line: fruits collected <10m from bowers; stars and dotted line: fruits collected >300m from bowers. In LMSU colour space what humans call hue is represented by the angle a point drawn to the origin subtends on the axes (up = red, clockwise through green, blue, uv), and what we call 'chroma' or 'purity' is represented by the distance from the origin. The fruit found on bowers is slightly greener and less chromatic than those found off the bowers, with fruit with higher chroma and relatively more yellow far from the bower. On bower vs. near fruit permutation test effect size = 0.08, $p < 0.0001$; on bower vs. far fruit effect size = 0.21, $p < 0.0001$, combined on and near bower fruit vs. far fruit effect size = 0.14, $p < 0.0001$.

surrounded by many *Solanum* plants the following year ($r_s = 0.55$, $n = 20$, $p = 0.009$; Supplemental information). Males with a local supply of *Solanum* fruit may benefit in a third way, spending less time away from the bower searching for fruit, thus reducing exposure to marauding by neighbours [5]. However, bower owners with more plants in their immediate vicinity did not spend more time at their bowers than those with few or no plants nearby ($r_s = -0.16$, $n = 23$, $p = 0.46$). The fruits do not provide direct nutritional benefits. We never observed bowerbirds eating them, and found no *Solanum* seeds in faecal samples [4].

S. ellipticum is a native, herbaceous, perennial pioneer species that becomes established where there is good sun, such as on the edges of forests or roadsides [6]. The plant benefits from collection by bowerbirds because their fruits are transported to unusually bare areas suitable for germination and pioneering establishment, with reduced competition for light, water and nutrients. Ground immediately surrounding bowers had lower grass and herb coverage than same sized patches of ground selected at random ($t_{38} = 2.19$, $p = 0.035$; Supplemental information). We have no direct evidence that males intentionally prepare or tend ground around their bowers. However, males clear leaf litter or foliage from around their bowers, perhaps to enhance visual contrast of decorations against their background [7] or reduce fuel loads, lessening risks from bush fire [8]. The byproduct of such behaviors, bare ground, provides an ideal habitat for the germinating *Solanum* seeds.

Cultivation may drive change in the visual properties of the fruit. Fruits from bowers had lower chroma and a slightly greener hue than those from plants far from the bower (Figure 1D). Fruit from the three locations all differed in spectral properties, but those taken from plants close (<10 m) to the bower were more similar in their spectral properties to those fruit on the bower than to fruit taken from plants far (>300 m) from the bower, and when fruit from on and near the bower were considered as a group, they differed from fruit from far from the bower (effect size = 0.14, $p < 0.001$). If fruit colour is heritable, then propagation of favoured fruit near the bower could lead to an accumulation of especially attractive fruit nearby. Decoration colour is important to bowerbirds, with males discriminating between even fine-scale gradations of colour in choice tests (e.g. [9]). Males at Taunton preferred *Solanum* fruit that were found on bowers to those from plants far from bowers, even when both were equally sized, aged and accessible (Wilcoxon signed ranks test, $n = 15$, $p = 0.044$).

By our using the term ‘cultivation’, we are not invoking any intent (although we cannot rule it out), and the process is likely indirect, being a by-product of the male’s maintenance of his bower, discarding fruits that have shrivelled and turned brown beyond the limits of his display. We have no evidence that the males actively alter either the fruits or the ground on which they are deposited, or that males preferentially tend *Solanum* plants in their local areas so as to enhance fruit yield. However, our observations of enhanced association between the bird and plant, yielding benefits to each, leading to co-evolutionary change in fruit colour, mirrors the processes suggested to have originated cultivation in humans [1]. Indirect cultivation is a novel example of niche construction [10] with the male bowerbird manipulating his local environment, reducing his costs of collecting important decorations in future years. A local, cultivated supply of these fruit may benefit the male, but the loss of discriminatory costs confounds one basis of choice for females.

Supplemental Information

Supplemental Information includes introductory information and two figures and can be found with this article online at doi:10.1016/j.cub.2012.02.057.

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