means better supported than the assumption that facultative mate choice in *S. bombifrons* females was selected for, and it is only presented here as a speculation to illustrate that presently we lack a genetic explanation for the choice results.

Will a change in female preference really affect relative mating frequencies in nature and, hence, explain the pond-to-pond differences in hybrid proportions?

In several anurans, female choice measured in twofold choice experiments cannot be realised in mating assemblies in natural ponds, partly because the acoustic environment is too complex to allow unambiguous discrimination and partly because female choice is overrun by competition among indiscriminately mating males [19–21]. Moreover, shallow and deep ponds are likely to differ in many more ways than just in the risk of desiccation. Variation might occur in population density, species ratios and sex ratios, abiotic factors and food resources, as well as in the surrounding community of competitors, predators and parasites. All these factors can, directly or indirectly, affect the ratio of conspecific versus heterospecific mating combinations and the proportions of surviving BB, BM and MM offspring.

Pfennig and her collaborators seem to have already collected most of the ecological, demographic, life-history and genetic data needed to answer a few of these questions [13–15]. It would be interesting to see all data combined and incorporated into a mathematical model. This could allow a quantitative test whether the cost/benefit ratio from hybridisation can really select for facultative mate choice, with a preference for heterospecific mates in ephemeral ponds. Whatever the outcome, the present study adds exiting new insights into sexual selection and the role of adaptive hybridisation.

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Letters

Animal-borne imaging takes wing, or the dawn of ‘wildlife video-tracking’

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Moll and colleagues [1] presented a timely review of the use of animal-mounted video cameras for basic and applied ecological research. We welcome the authors’ attempt to unveil the scientific potential of this emerging technology, but wish to highlight new research opportunities arising from the latest work with bird-mounted cameras.

For about two decades, marine biologists have used animal-borne video cameras on seals, sharks, whales

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and other species [2,3], but until very recently, units were far too heavy for most terrestrial applications [1]. The discussion by Moll *et al.* reflects the field's historical roots, and leaves readers with the impression that state-of-the-art camera systems weigh 1.5–2.0 kg, with the smallest attainable devices being 240 g (Box 1 and Table 1 in Ref. [1]). The authors observe that smaller video cameras are now commercially available, but are concerned that "adapting them into field-worthy [tags] will take time." However, several independent research teams have recently developed camera systems for avian deployment that are well below 80 g [4–7]. At a weight of only 14 g, the smallest units to date [4] (Figure 1) are suitable for a wide range of birds, mammals and reptiles. The transition of the technology from water to land not only dramatically increases the number of candidate species for camera tagging but presents the community with a chance to explore innovative ways of using animal-borne video. This demands a rethinking process, which we hope to initiate with the discussion offered below.

Although Moll *et al.* emphasize the general value of integrating video with other technologies, they do not foresee how easily this can be achieved in terrestrial applications. We believe animal-borne imaging is particularly useful when video is collected simultaneously with positional tracking data from a single, integrated animal-borne unit—a technique we call 'wildlife video-tracking' [4]. At the analysis stage, video scenes are linked to radio-fixes, yielding an animal's-eye view of resource use and social interactions along a known movement trajectory. This approach was pioneered by marine biologists (e.g. Refs [3,8]) but has not been widely used, possibly because reconstructing 2D or 3D trajectories for aquatic subjects is logistically and technically challenging. By contrast, the habitat and lifestyle of terrestrial animals makes positional tracking particularly productive, and there are excellent options for cheap (VHF radio-telemetry) or high-resolution data collection (GPS loggers) [9]. Furthermore, land animals typically range across well-defined, easily mapped habitat types, facilitating data analysis and interpretation [9]. The latest research with bird-mounted cameras [4–7] has created opportunities to exploit these advantages by merging novel video technology with well-established, efficient tracking techniques.

Video-tracking is suitable for a wide range of applications [4], but its key strength is putting animal behaviour into an explicit spatio-temporal context. In general studies of animal ranging behaviour, it will provide precious biological information for radio-fixes [1] and enable researchers to quantify how certain behaviours vary across habitat types [4]. But we also envisage more specific studies that use the technique to follow predators during individual hunting trips, recording their attack decisions, or to map social interactions in species with complex fission–fusion dynamics. The video-transmission time of integrated video-tags for birds (Figure 1) is currently in the order of hours, which might seem short. With the quantitative deployment of such tags, however, most laboratories will quickly accumulate more high-quality footage than they can analyse. Moreover, the integrated VHF radio-tag of units (Figure 1a) lasts for weeks after the video circuit expires, providing sufficient time to collect data for conventional home-range and habitat-use analyses [9].

Figure 1. Animal-borne video cameras for wild, free-flying birds [4]. **(a)** Integrated video-tag ready for deployment (mass = 13.57 g), containing two independent transmitter systems: (i) a conventional VHF radio-tag for positional tracking (long, thin antenna; battery life *ca.* 3 weeks) and (ii) a 2.4 GHz transmitter for video and audio transmission (short, thick antenna; battery life *ca.* 70 min). **(b)** Wild New Caledonian crow (*Corvus moneduloides*) fitted with an integrated video-tag. The camera lens is protruding through the central tail feathers, providing a bird's-eye view of the environment. Photo credits: (a) Lucas A. Bluff; and (b) Jolyon Troscianko.

We agree with Moll *et al.* that the field would benefit from the commercial availability of equipment, but propose that the most urgent step for promoting this young technology is to share knowledge and expertise freely within the community [10]. This, in combination with accelerating technological advancement, will ensure that animal-borne imaging becomes firmly established as a powerful tool for quantitative, hypothesis-driven research. The next few years will see the development of even smaller video-tags and of miniature solid-state video-loggers. Using trained birds, experimental biologists are already paving the way for GPS-based video-tracking and sophisticated, multisensor data collection from wild subjects.

We encourage terrestrial ecologists to incorporate animal-borne imaging into their current projects. Even with existing technology, they will enjoy fresh biological insights into their study systems, and together, the community will become a major force in pushing technological frontiers in wildlife research.

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Letters Response

A pragmatic view of animal-borne video technology

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Based on recent applications to wild and trained birds [1–3], Rutz and Bluff highlighted developments in animal-borne video and environmental data collection systems (AVEDs) [4]. We agree that AVEDs can provide novel insights relevant to behavioural ecology and conservation [5]. Their emphasis on video-tracking reinforces our broader recommendations about the utility of combining video with other sensors [5]. However, Rutz and Bluff give ecologists an overly optimistic view of transmission-based AVEDs and video-tracking. In addition, by simply encouraging "terrestrial ecologists to incorporate animal-borne imaging into their current projects," they unintentionally reinforce our concern that ecologists will focus too much initially on technology-driven objectives when using AVEDs [5]. We encourage a more pragmatic view of terrestrial AVED technology, one that considers tradeoffs and limitations of available AVEDs in the context of underlying research objectives.

The transmission-based AVEDs promoted by Rutz and Bluff provide a good context for discussing the types of tradeoffs that ecologists should consider. Currently, these systems are light enough to deploy on birds such as crows (*Corvus spp.*) [1]. However, there are several limitations that must be considered. These AVEDs transmit video to an external data storage device which results in severe logistical constraints for most species. A video-transmitter using a small power source cannot transmit energy over a long distance – typically no more than a few hundred yards. Signals from small video-transmitters are attenuated by foliage, moisture, power lines, buildings and other factors, so the researcher must maintain close contact to receive video. Our research demonstrates that when an animal moves out of range or within an area that the signal cannot penetrate, video data are lost and battery power is wasted [6]. Further, manual tracking risks disruption of tagged animals, possibly biasing data or even adversely affecting these animals. Moreover, it is often difficult to maintain close contact with many wild animals given limitations in line-of-sight radio-tracking technology [7] and the elusive nature of animals that range over large areas. Yet, these are the species for which AVEDs are most valuable.

Small, transmission-based AVEDs [1] also are limited by the length of time a tag will transmit video. Many research questions (e.g. valuating predator hunting decisions and mapping social interactions in complex systems [4]), particularly those related to rare behaviours (e.g. feeding events in sharks [8]), require substantial recording time. Animal-borne sensors should weigh <3–5% of the animal's body mass [5]; for small animals, this means the mass of AVEDs limits the size and battery life of the radio-transmitter used for radio-tracking. A researcher must

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