Bioacoustic monitoring of animal vocal behavior for conservation

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Abstract
The popularity of bioacoustics for threatened species monitoring has surged. Large volumes of acoustic data can be collected autonomously and remotely with minimal human effort. The approach is commonly used to detect cryptic species and, more recently, to estimate abundance or density. However, the potential for conservation-relevant information to be derived from acoustic signatures associated with particular behavior is less well-exploited. Animal vocal behavior can reveal important information about critical life history events. In this study, we argue that the overlap of the disciplines of bioacoustics, vocal communication, and conservation behavior—thus, “acoustic conservation behavior”—has much to offer threatened species monitoring. In particular, vocalizations can serve as indicators of behavioral states and contexts that provide insight into populations as it relates to their conservation. We explore the information available from monitoring species’ vocalizations that relate to reproduction and recruitment, alarm and defense, and social behavior, and how this information could translate into potential conservation benefits. While there are still challenges to processing acoustic data, we conclude that acoustic conservation behavior may improve threatened species monitoring where vocalizations reveal behaviors that are informative for management and decision-making.

KEYWORDS
bioacoustics, conservation behavior, monitoring, vocal behavior, vocalizations

1| INTRODUCTION

Bioacoustic monitoring is a rapidly emerging tool in wildlife conservation, aided by recent advances in technology and analytical approaches (Snaddon, Petrokofsky, Jepson, & Willis, 2013). Distinct from the related discipline ecoacoustics, bioacoustics is behavior-centric and focuses on the acoustic signals of individuals and species, rather than broader ecological processes or environments (Sueur & Farina, 2015; Towsey, Parsons, & Sueur, 2014). Potentially suited to any sound-producing species, especially those that are rare, cryptic or otherwise difficult to observe (Williams, O’Donnell, & Armstrong, 2018; Wrege, Rowland, Keen, & Shiu, 2017; Zwart, Baker, McGowan, & Whittingham, 2014), bioacoustic monitoring via autonomous recording units is becoming increasingly popular for measuring metrics such as species presence–absence (Sebastián-González, Pang-Ching, Barbosa, & Hart, 2015; Zwart et al., 2014), species richness (Celis-Murillo, Deppe, & Ward, 2012; Wimmer, Towsey, Roe, & Williamson, 2013), abundance (Borker et al., 2014; Jaramillo-Legorreta et al., 2017), and density (Efford, 2011; Efford & Fewster, 2013; Lambert & McDonald, 2014; Marques et al., 2013; Rogers, Ciaglia, Klinck, & Southwell, 2013; Stevenson et al., 2015).

In contrast, bioacoustics is not commonly used to monitor animal behavior, despite the extensive literature on animal acoustic communication and vocal behavior (Bradbury &
TABLE 1  Examples from the literature summarizing the potential benefits of bioacoustic monitoring programs of animal behavior over traditional methods

| Challenges of traditional monitoring | Potential benefit of bioacoustic monitoring | Example application |
|--------------------------------------|-------------------------------------------|---------------------|
| Individuals are difficult to observe or habitat is difficult to access | Improved detection of individuals | Amphibian Gladiator frog, *Hypsiboas rosenbergi* | LC Male chorusing | Relative importance of environmental and social cues to reproduction | Höbel (2017) |
| | | Mammal Sperm whale, *Physeter macrocephalus* | VU Social clicks and foraging clicks | Social and foraging time budget (ratio of hours per day). Spatial and temporal variation | E. M. McDonald, Morano, DeAngelis, and Rice (2017) |
| | | Bird White-bellied heron, *Ardea insignis* | CR Breeding calls | Variation in breeding activity among nesting sites | Dema et al. (2018) |
| | | Behavior of interest is difficult to observe or measure | Improved ability to monitor cryptic or rare behaviors | Amphibian Olive frog, *Babina adenopleura* | LC Individually distinct male advertisement calls and aggression calls | Variation in aggression towards neighbors and strangers (dear enemy effect) | Chuang, Kam, and Bee (2017) |
| | | Mammal African elephant, *Loxodonta africana* | VU Rumbles | Translocation-induced stress (validated from fecal glucocorticoid metabolite levels) | Viljoen, Ganswindt, Reynecke, Stoeger, and Langbauer (2015) |
| | | Mammal Forest elephant, *Loxodonta cyclotis* | NA Rumbles | Diel changes in behavior relative to seismic oil exploration | Wrege, Rowland, Thompson, and Batruch (2010) |
| | | Mammal Killer whale, *Orcinus orca* | DD Call use within matrilines | Birth of calves | Weiß, Ladich, Spong, and Symonds (2006) |
| | | Mammal Chimpanzee, *Pan troglodytes* | EN Long-distance pant-hoot calls and non-vocal drumming | Changes in ranging behavior (centre of activity) | Kalan et al. (2016) |
| | High resource requirements (e.g., human hours, cost) to obtain sufficient data | Improved efficiency, cost-effectiveness or coverage (spatial or temporal) | Bird White-backed vulture, *Gyps africanus* | CR Alarm calls of meerkats, *Suricata suricatta*, given when vultures are sighted | Population trend through time | Thorley and Clutton-Brock (2017) |
| | | Amphibian Richmond range mountain frog, *Philoria richmondensis* | EN Male advertisement calls | Breeding phenology through time and relationship with abiotic factors | Willacy, Mahony, and Newell (2015) |
| | | Bird Australasian bittern, *Botaurus poiciloptilus* | EN Male boom calls | Number of calling males. More cost-effective than human observers | Williams et al. (2018) |
This is unfortunate because vocalizations of anurans, birds, and mammals are often well-described for critical behaviors like reproduction and defense (Bradbury & Vehrencamp, 2011). Knowledge on vocal behaviors can contribute to conservation outcomes if those behaviors provide insight into a population that exposes a conservation problem or monitors responses to conservation actions. We propose, therefore, that bioacoustic monitoring programs should give greater consideration to animal behavior (Table 1). For some species, bioacoustics may be the only feasible approach with which to acquire behavioral data, such as for cetaceans’ cryptic behaviors (E. M. McDonald et al., 2017). Bioacoustics may also be more efficient and cost-effective than traditional methods (Williams et al., 2018).

The discipline of conservation behavior seeks to apply behavioral knowledge to conservation solutions. Although a relatively young discipline, several books have been published on the topic (Berger-Tal & Saltz, 2016; Blumstein & Fernández-Juricic, 2010; Buchholz & Cleemons, 1997; T. M. Caro, 1998; Festa-Bianchet & Apollonio, 2003; Gosling & Sutherland, 2000), and its scope and utility have received considerable attention in recent literature (Angeloni, Schlaepfer, Lawler, & Crooks, 2008; T. Caro, 1999, 2016; T. Caro & Sherman, 2011, 2013; Harcourt, 1999; Knight, 2001; Linklater, 2004). Early on, conservation behavior research tended to focus on behaviors that affect population persistence (Anthony & Blumstein, 2000), while recent studies have commonly examined behavioral responses to anthropogenic impacts (Barber, Crooks, & Fristrup, 2010; Laiolo, 2010; Owens, Stec, & O’Hatnick, 2012; Shannon, Angeloni, Wittemyer, Fristrup, & Crooks, 2014; Slabbe Koorn & Ripmeester, 2008; Templeton, Zolting, & Brumm, 2016). To better define the application of animal behavior to conservation, Berger-Tal et al. (2011) proposed a framework of three interconnected conservation themes to which behavior is relevant. These themes are defined as: (1) anthropogenic impacts on animal behavior, which can alter the fitness of individuals; (2) behavior-based management, in which managers aim to preserve or change a species’ behavior (e.g., pre-translocation anti-predator training); and (3) behavioral indicators, whereby the behaviors themselves are a source of information about the state of a species or its habitat. Theme 3 pertains to monitoring, which is most relevant to bioacoustic studies of animal behavior. Specifically, by monitoring vocal

| Challenges of traditional monitoring | Potential benefit of bioacoustic monitoring | Example application |
|--------------------------------------|--------------------------------------------|---------------------|
| Mammal | Southern yellow-cheeked crested gibbon, Nomascus gabriellae | EN | Morning calls | Spatial variation in occupancy. More efficient than human observers in habitats with low gibbon density | Vu and Tran (2019) |
| Bird | Rock ptarmigan, Lagopus muta | LC | Individually distinct male breeding songs | Abundance estimate. Relative to point-counts, acoustic methods reduced observer bias and double-counting of individual birds | Marin-Cudraz et al. (2019) |
| Bird | Western Capercaillie, Tetrao urogallus | LC | Male lek calls | Number of males at lek sites, estimated from call rate per site. Comparison of bioacoustic and observer data suggests human disturbance may affect counts | Abrahams (2019) |

Note that several challenges or benefits are likely to apply to any given monitoring program.
behaviors that indicate the state of individuals or groups for metrics that are relevant to conservation (e.g., reproductive status), populations and their trends can be tracked to inform decisions.

Under Theme 3, Berger-Tal et al. (2011) provides two pathways that link behavioral domains to conservation outcomes. First, behaviors can reveal threatening processes and act as warning systems for population declines. Vocal behaviors may, for example, signal habitat quality or reproductive success. In the Eurasian eagle owl, Bubo bubo, males with the greatest fecundity and proportion of rats in the diet called significantly earlier during the dusk chorus (Penteriani, Delgado, Stigliano, Campioni, & Sánchez, 2014). Vocal behaviors like these may reveal areas where reproduction is relatively poor, even if many individuals persist there. For species whose behaviors are socially transmitted, the size of groups that a habitat can support may be critically important. Fragmented populations may see the loss of important behaviors (cultural erosion) which can cause declines faster than would otherwise be expected (Hart et al., 2018; Laiolo & Jovani, 2007; Laiolo & Tella, 2007). In this capacity, habitat ought to support not just a species' presence, but also the presence of behaviors that facilitate its long-term viability. Bioacoustics may serve to acquire this knowledge. Second, behaviors can provide a means to monitor and evaluate the effectiveness of conservation actions. This process of evaluation is critical for effective conservation planning and adaptive management (Lindenmayer, Piggott, & Wintle, 2013). Monitoring vocal behaviors may facilitate this by examining temporal and spatial trends in behaviors that indicate key life-history stages. An example of this would be examining changes in a population's breeding success, such as via the presence of infants' vocalizations, over time following conservation action.

In this review, we examine the potential benefits to conservation from the bioacoustic detection of animal vocal behavior. We consider vertebrate vocalizations that may facilitate conservation monitoring, namely those associated with reproduction and recruitment, alarm and defense, and social behavior (Table 2). The challenges of processing large acoustic datasets are discussed. We conclude saying that monitoring vocal behavior using bioacoustics has much to offer conservation, provided that monitoring programs are explicit in their objectives and the link between them and the vocalizations detected.

2 | VOCAL BEHAVIOR AND CONSERVATION

2.1 | Reproduction and recruitment

Understanding how a species' reproductive behaviors and breeding success differ among various levels of habitat perturbation can be informative for protected area planning or habitat restoration. If vocalizations reveal that certain environments consistently comprise individuals with poorer reproductive success, then decisions can be made about improving habitat or, alternatively, focusing conservation efforts elsewhere. In male songbirds, mate attraction is a chief function of singing, as is territory defense (Catchpole & Slater, 2008; Marler & Slabbekoorn, 2004; Nowicki & Searcy, 2005). Sexual selection can act strongly on males' songs, since for many species females choose males according to song characteristics (Andersson, 1994). Song complexity, singing rate, singing duration and repertoire size have been shown to influence females' behaviors (Catchpole & Slater, 2008). Moreover, since singing is physically challenging, higher quality males, or those occupying higher quality territories, should sing songs that are closer to a physiological performance limit (Liu et al., 2017; Nowicki & Searcy, 2005). This can lead to a reproductive advantage. In the song sparrow, Melospiza melodia, for instance, high-performance songs (a measure of frequency bandwidth relative to trill rate; Podos et al., 2016) induce more copulation solicitation displays from females (Ballentine, Hyman, & Nowicki, 2004). Males with larger vocal repertoires also maintain larger territories and have greater annual and lifetime reproductive success (Hiebert, Stoddard, & Arcese, 1989). In such cases, monitoring song traits may help to define the environmental factors that support high quality males and reproductive success. Equally, the occurrence of males with poor fitness may be vocally indicated, thus highlighting poorer population outcomes (McGregor, Peake, & Gilbert, 2000).

In mammals, body size is a sexual trait that is commonly signaled in males' reproductive vocalizations, and many studies highlight females' preference for larger males; thus, vocalizations that signal body size may indicate fitness. Acoustic allometry shows that larger animals produce lower-pitched calls, since vocal production is highly constrained by the size of the vocal organs and vocal tract (Bowling et al., 2017; Fletcher, 2004). Information about body size (among other factors) may be contained in the fundamental (i.e., lowest) frequency of the vibration generated in the larynx (the source) or in the formant frequencies (amplified frequency bands adjacent to the fundamental frequency) generated via resonance filtering of the fundamental frequency through the vocal tract (the filter) (for a review of source-filter theory in mammals see Taylor and Reby (2010)). In playback experiments, female koalas, Phascolarctos cinereus, and red deer, Cervus elaphus, prefer male vocalizations that contain formants that indicate a large body size (Charlton, Ellis, Brum, Nilsson, & Fitch, 2012; Charlton, Reby, & McComb, 2007). In bison, Bison bison, the bellows of larger males contain lower frequency
A recent study on banded penguins, *Spheniscus* sp., found that the ecstatic display song given by males during the breeding season encodes body size in the fundamental frequency (Favaro, Gamba, Gili, & Pessani, 2017). Male little blue penguins, *Eudyptula minor*, produce growl vocalizations that vary significantly in peak frequency with body size (Miyazaki & Waas, 2003). Larger males produce eggs and chicks earlier in the season, and their chicks grow faster.

Vocalizations can also provide direct measures of reproductive contexts or events. Many animals vocally announce reproductive events (e.g., foraging, fission–fusion, demographic composition), improve parameterization of predictive models, and determine if, and how often, groups interact. Inform whether groups should be treated individually or collectively for management. Spatial and temporal variations in vocalizations can also provide direct measures of reproductive success, as they can signal the presence of juveniles in groups by way of the lower-pitched vocalizations of smaller-bodied individuals.

**TABLE 2** Summary of vertebrate vocal behaviors that are relevant to conservation

| Behaviors represented | Reproduction and recruitment | Alarm and defense | Sociality and vocal complexity |
|-----------------------|------------------------------|------------------|-------------------------------|
|                       | Vocalizations for mate attraction | • Conspicuous vocalizing to warn conspecifics of predators | • Group behaviors and contexts, for example, foraging, fission–fusion, demographic composition |
|                       | Complex calls or songs | • Aggression | • Vocal convergence within and between groups |
|                       | Reproductive events (e.g., copulation, birth) | | • Cultural transmission of critical behaviors |
|                       | Infant and juvenile calling | | |
|                       | Infant and juvenile begging | | |
| Relevance to conservation | Define the habitats or other environmental factors that support high-quality males and reproductive success | Monitor predator presence or abundance via prey species’ alarm calls | Improve resolution of demographic data, such as age and gender composition of groups |
|                       | Provide direct measure of reproductive events | Provide an index of the cost of defense, for example, reduction in foraging | Improve parameterization of predictive models |
|                       | Signal the presence of juveniles in groups by way of the higher-pitched vocalizations of smaller-bodied individuals | Measure the level of threat from competitive species | Determine if, and how often, groups interact. Inform whether groups should be treated individually or collectively for management |
|                       | Quality or health of juveniles | Spatial and temporal variations | Spatial and temporal variations |
|                       | Spatial and temporal variations | | |
| Key principles | Sexual selection for call complexity: females prefer complex calls or songs, as they indicate high-quality males | Functionally referential alarm calls: calls refer to, and possibly convey information about, a specific external threat and they elicit in receivers antipredator behaviors that can be repeated in isolation | Social complexity hypothesis for vocal communication: animals that live in complex societies exhibit complex vocal repertoires |
|                       | Acoustic allometry: vocalizations vary by body size | | Vocal convergence: associated individuals share calls that are distinct from other social groups. May manifest as regional or geographical dialects |
|                       | Sexual selection for body size: females prefer larger males | | Culturally significant units |
|                       | Infant and juvenile begging: individuals beg more when hungry or if they are of higher metabolic quality | | |
| Key references | Catchpole and Slater (2008) | Seyfarth, Cheney, and Marler (1980a, 1980b) | Freeberg, Dunbar, and Ord (2012) |
|                       | Fletcher (2004) | Smith (2017) | Kershenbaum and Blumstein (2017) |
|                       | Charlton and Reby (2016) | Townsend and Manser (2013) | Tyack (2008) |
|                       | Godfray (1991) | Macedonia and Evans (1993) | Conservation of Migratory Species of Wild Animals (2017) |
|                       | Johnstone and Godfray (2002) | | Ryan (2006) |
|                       | Mock (2016) | | Whitehead, Rendell, Osborne, and Würsig, (2004) |
their readiness to mate, often in conspicuous displays. Like songbirds, male frogs are well known for their advertisement calls during the breeding season, and these can be monitored in relation to local environmental factors (Plenderleith et al., 2017) or latitudinal gradients (Lowe, Castley, & Hero, 2016), which may help to predict how a species' breeding output will be affected by environmental change. Furthermore, vocal activity may indicate reproductive success (Höbel, 2017), including how these differ over time or among areas. Conspicuous vocal signals may also accompany copulation events in some species. In African elephants, Loxodonta africana, copulation is signaled by way of the loud and overlapping calls made by many members of the female's family, for which scientists have termed it “the mating pandemonium” (Payne, 2003; Poole, 2011). Within a given area, these loud vocalizations could presumably serve to measure copulation events directly. Chimpanzees, Pan troglodytes, most often females, also exhibit copulation vocalizations. These behaviors are given significantly more when a female is with a high-ranking male, and are suppressed when in the presence of high-ranking females (Townsend, Deschner, & Zuberbühler, 2008). However, the number of copulations does not necessarily indicate habitat quality or recruitment into populations. These assumptions should be tested if copulations are to provide an index of reproductive success or its relationship to habitat factors.

Other vocalizations may provide more direct measures of recruitment. If vocalizations accompany parturition or fledging, success rates could be estimated from monitoring these vocalizations. In killer whales, Orcinus orca, calling behavior within matriline (mothers and descendants) groups changes markedly after the birth of a calf (Weiß et al., 2006). Additionally, in mammals, infants' first vocalizations provide a direct measure of birth success. For example, observations of a barbary macaque, Macaca sylvanus, show changes in a female's moans as labor progresses (increasing in frequency and regularity), and the screaming of the infant following birth (Hammerschmidt & Ansome, 1989). These may act as acoustic signals of recruitment into populations.

In some species, vocalizations may signal the presence of infants or juveniles in groups. Among birds and mammals, it is common for infants and juveniles to learn vocalizations from adults. During learning, the calls of young individuals can be highly variable. For example, in cotton-top tamarins, Saguinus oedipus, the variability in the structure of food-associated vocalizations is higher in infants than in sub-adults and adults (Roush & Snowdon, 2001). Infants' food-associated repertoire decreases over time as they learn which vocalizations are relevant to feeding. Likewise, in leopard seals, Hydrurga leptonyx, juveniles' vocalizations are less stereotyped than those of adult males, and their repertoires are larger (Rogers, 2007). These differences have allowed for the study of age-related differences in spatial distribution, which is otherwise unfeasible with visual surveys (Rogers et al., 2013). The presence of juveniles in a group may also be indicated by changes in the composition or rate of a group's calls. In the meerkat, Suricata suricatta, the call rate of the adults' close contact calls decreases when pups are foraging with the group, presumably a response to the loud and continuous begging calls given by the pups (Wyman, Rivers, Muller, Toni, & Manser, 2017). Additionally, since frequency is strongly affected by the size of the individual's vocal anatomy, the presence of young individuals in a group may be detectable by the greater acoustic energy at higher frequencies. This approach predicts the presence of pups in packs of the Iberian wolf, Canis lupus signatus (Palacios, Lopez-Bao, Llaneza, Fernandez, & Font, 2016). While such a method requires further study in other species, it may prove to be a reliable and simple mechanism by which the presence, and potentially the abundance, of juveniles in a group could be estimated without disturbance from an observer.

Finally, vocalizations can signal not only reproductive success but also the quality or health of infants or juveniles. Again, these may vary by habitat factors that could be improved through management. The vocalizations of infant birds and mammals, which are often conspicuous and extravagant, may encode signals that vary with individual states, such as hunger. A pertinent example is begging in young birds and mammals, a behavior that is thought to function largely as signals of an individual's need or quality (Hinde & Godfray, 2011; Johnstone & Godfray, 2002). Evidence of the former comes from the many experiments that show hungrier infants to vocalize differently, usually louder or more often (Gladbach, Büßer, Mundy, & Quillfeldt, 2009; Godfray, 1991; Klenova, 2015; Manser, Madden, Kunc, English, & Clutton-Brock, 2008; Rector, Walsh, Kowenber, Fitzsimmons, & Storey, 2014; Redondo & Castro, 1992; Reers & Jacot, 2011). Parents or other adults may respond with greater food provisioning. For example, in cooperatively breeding meerkats, food-deprived pups beg at greater rates, to which adults respond by increasing food allocation to the hungry pups (Manser et al., 2008). Furthermore, food calls and provisioning vocalizations are known from many birds and mammals (Evans & Evans, 2007; P. G. McDonald & Wright, 2008; Roush & Snowdon, 2001), which could provide information on food availability and use (Suzeaki & Kutsukake, 2017), or even direct measures of feeding events. For example, most cockatoo species (family Cacatuidae) exhibit juvenile food-swallowing vocalizations, given during food transfer (allofeeding) from parent to young (Courtney, 1996). In the golden lion tamarin, Leontopithecus rosalia, adults use food-offering calls to encourage juveniles to take prey and later, as juveniles learn
foraging skills, to assist with directing juveniles to prey locations (Rapaport, 2011). Use of foraging habitat or rate of feeding events may differ among individuals and habitat types (e.g., quality), which may relate to factors in the environment that could be managed.

The honesty of begging signals is hypothesized to be maintained by the associated metabolic and predation costs (Haff & Magrath, 2011; Ibáñez-Álamo, Arco, & Soler, 2012; Kilner, 2001; P. G. McDonald, Wilson, & Evans, 2009; Recttor et al., 2014; Rodríguez-Gironés, Zúñiga, & Redondo, 2001). Indeed, parental alarm calls may suppress infants' vocalizations, such as in the white-browed scrubwren, Sericornis frontalis (Platzen & Magrath, 2004). Alternatively, “begging” may actually be “boasting”; that is, high-quality juveniles, who are metabolically more capable, produce conspicuous vocalizations that may facilitate parental provisioning to the strongest young, depending on environmental conditions (S. M. Caro, Griffin, Hinde, & West, 2016; Mock, 2016). In either case, differences in the state of juveniles between areas can help managers decide where actions to improve breeding outcomes are needed, such as by increasing the extent or quality of food resources near breeding sites, or evaluate the success of management interventions.

### 2.2 Alarm and defense

The vocalizations associated with alarm and defense may offer conspicuous vocal signals that can be easily detected in bioacoustic studies. A novel approach that can benefit conservation monitoring is to use prey species' alarm calls as a proxy of predator abundance. For example, in Australia, sugar gliders, Petaurus breviceps, are a major nest predator of the critically endangered swift parrot, Lathamus discolor (Stojanovic, Webb, Alderman, Porfirio, & Heinsohn, 2014). In a recent study, the occupancy of sugar gliders in the swift parrot's breeding habitat was estimated by eliciting gliders' alarm calls from playback of the calls of southern boobook owls, Ninox novaeseelandiae, which depredate the gliders (Allen, Webb, Alves, Heinsohn, & Stojanovic, 2018). Similarly, in South Africa's Kalahari, the decline of the white-backed vulture, Gyps africanus, over 17 years was estimated from the occurrence of alarm calls that sympatric meerkats give upon sighting a vulture (Thorley & Clutton-Brock, 2017).

Indeed, for some species the alarm call can be highly specific to the threat, thereby improving the resolution of threat-specific data, in which case the calls are termed “functionally referential.” By definition, functionally referential calls meet two criteria: (a) they refer to, and possibly convey information about, a specific external threat and (b) they elicit in receivers antipredator behaviors that can be repeated in isolation (Macedonia & Evans, 1993; Smith, 2017; Suzuki, 2016; Townsend & Manser, 2013). In early seminal studies, Seyfarth et al. (1980a, 1980b) showed that vervet monkeys, Chlorocebus aethiops, produce unique alarm calls for eagles, leopards and snakes, to which receivers respond with unique antipredator behaviors: monkeys look up or run for cover in response to “eagle” alarm calls, run up trees in response to “leopard” alarm calls, and look down or approach the predator in response to “snake” alarm calls. Urgency of the threat may also be signaled, as in the graded alarm calls of the meerkat (Manser, 2001). Functionally referential alarm calls have been reported for several other primate and non-primate mammals (Townsend & Manser, 2013), as well as birds from several families (Gill & Bierema, 2013; Smith, 2017). It is possible, therefore, that for some species alarm calls could provide an index of the costs of specific threats, such as the frequency of fleeing for cover from predators. These costs may be substantial, for instance, if they interfere with important behaviors like foraging. In the blue tit, Cyanistes caeruleus, the presence of model sparrowhawk incited a decrease in foraging and an increase in vocalization and wing-flicking (Carlson, Pargetter, & Templeton, 2017), all of which would incur an energetic cost.

Alarm calling can also indicate aggression, which itself may be a threat to some species. For instance, noisy miners, Manorina melanocephala, produce functionally referential alarm calls for airborne and non-airborne predators, which elicit unique behavioral responses from receivers (Cunningham & Magrath, 2017; Farrow, Doohan, & McDonald, 2017). Mobbing (a deterrent behavior) is an aggressive and vocally conspicuous response to non-airborne predators and competitors (Cunningham & Magrath, 2017), which is suggested as a reason for the negative relationship between bird species richness and miner abundance (Kutt, Vanderduys, Perry, & Perkins, 2012). By monitoring the alarm calls associated with mobbing, bioacoustics could produce a relatively straightforward way to monitor the occurrence of this behavior. This would help to gauge the severity of this threat among habitats that vary in disturbance level or other factors.

### 2.3 Sociality and vocal complexity

Sociality begets complexity, and animals that live in complex societies are thought to exhibit more complex vocal repertoires because they have more social interactions to navigate. Pro-social behaviors, like cooperation, collaboration, and reciprocity (Krams, Krama, Freeberg, Kullberg, & Lucas, 2012) are posited to be facilitated by complex vocal abilities (Freeberg et al., 2012; Freeberg & Krams, 2015). Termed the social complexity hypothesis for vocal communication (Freeberg et al., 2012; Kershenbaum & Blumstein, 2017), it is supported both in primates and birds (Leighton, 2017; McComb & Semple, 2005). In social species,
therefore, vocalizations can indicate a greater range of behavioral and demographic contexts, such as group size or composition by age and gender. Depending on the conservation issue being examined, vocal signals may improve the resolution of datasets and predictive models (e.g., population viability analysis). For example, in sperm whales, *Physeter macrocephalus*, E. M. McDonald et al. (2017) calculated group-level behavioral time-budgets according to the ratio of clicks given in social situations versus those given during foraging. Based on previous descriptions of vocal behaviors (Whitehead & Weilgart, 1991), differences in this ratio between sites is suggested to indicate demographic differences, while temporal changes likely reveal differences in food availability. Similarly, in African savanna elephants, the occurrence of three call types (single voice, clustered, and high frequency) increases significantly with the complexity of group composition, from bull-only groups, to single family groups, to multi-family groups (Payne, Thompson, & Kramer, 2003).

Another important aspect of social behavior, as it relates to conservation monitoring, is vocal convergence, where associated individuals share one or more call types that are distinct from other conspecifics. These “affiliative” group-level vocal signatures are present in many social species (Tyack, 2008) and can indicate the segregation of species into distinct social groups or subpopulations. These may reflect variations in a species' cultural diversity, including reproductive boundaries, which could imply a need for management at sub-specific levels. For instance, the three sympatric but culturally and acoustically distinct killer whale, *O. orca*, groups (ecotypes) that exist in British Colombia are treated separately for conservation purposes (Conservation of Migratory Species of Wild Animals, 2017; Yurk, 2005). Likewise, acoustic distinctions are genetically supported in subpopulations of Bigg’s (“transient” ecotype) killer whale in western Alaska (Sharpe, Castellote, Wade, & Cornick, 2017). While vocal convergence may or may not reflect genetic boundaries (Bradbury, 2003), regional or geographical dialects can indicate the degree to which groups interact, and therefore inform management. For example, contact calls of the palm cockatoo, *Probosciger aterrimus*, vary graphically, and the most distinct contact call occurs in a population thought to have undergone long-term isolation (Keighley, Langmore, Zdenek, & Heinsohn, 2017). Thus, the management of this population should be considered separately. For the humpback whales, *Megaptera novaeangliae*, of Oceania, differences in males’ songs reveal that some populations (vocal clusters) form part of a metapopulation with some, albeit infrequent, interaction, while the east Australian whales are vocal and social outliers (Garland et al., 2015). Thus, vocal convergence may help to explain not only whether groups are socially distinct but also if, and how often, they interact. Moreover, the importance of preserving culture (socially learned behaviors) within groups of social species, termed “culturally significant units,” is increasingly recognized (Kühl et al., 2019; Ryan, 2006; Whitehead et al., 2004). Culture can govern the transfer of critical knowledge among individuals, the loss of which may perpetuate extinction risk faster than population size or genetic diversity predicts (Whitehead, 2010). For behaviors that are vocally facilitated, bioacoustics may provide an important tool to monitor cultural maintenance or erosion and the relationships to human impacts or other environmental factors (Kühl et al., 2019).

### 3 | CHALLENGES AND CONSIDERATIONS FOR BIOACOUSTIC MONITORING PROGRAMS

The increasing accessibility of bioacoustic technology risks providing massive volumes of sound data that do not accord with, or are in excess of, a program’s aims. To improve the manageability of bioacoustic programs, aims and objectives should be made explicit before a monitoring regime is established. Subsequently, the relevant vocal behaviors can be identified and the regime designed accordingly. Depending on existing knowledge, practitioners may need to examine and define the vocal behaviors that pertain to the program’s aims. In this capacity, practical considerations should include the position and detection range of the sound recorders used, as well as the frequency with which the recorders will need to be serviced for power and data storage. For example, if a program aims to measure nest survival in a bird species, practitioners should consider whether loud vocalizations, as opposed to soft close-range calls (e.g., between parents and offspring in the nest), provide sufficient data to achieve the program’s aims. If so, sound recorders may be placed at greater distances from the nests, which may improve practicality, and a lower sampling rate, which conserves memory and power, could be used. Efficiency can be further improved if these vocalizations can be temporally stratified or subsampled, either in the recording schedule used (i.e., time recorded per day, if the behaviors are thereby representative) or post hoc during data processing (Wimmer et al., 2013). Informed by explicit aims, monitoring programs should be designed to record appropriate vocal behaviors while maximizing efficiency.

Bioacoustic monitoring is only useful if the effort required to collect and process the data is less than that of human observers. Since bioacoustic monitoring typically generates very large volumes of sound data, algorithms to detect vocalizations from sound files, termed call recognizers, are critical to the success of bioacoustics as a wildlife
monitoring tool. The reliability of recognizers, however, has been mixed, performing well for some species and poorly for others. Performance depends in part on extraneous sources of sound (e.g., other species' calls) and the overall noisiness of the environment (e.g., anthropogenic noise, wind, rain), as well as the acoustic structure of the vocalizations, which is important in the choice of algorithm (Brandes, 2008; Cragg, Burger, & Piatt, 2015; Priyadarshani, Marsland, & Castro, 2018; Salamon et al., 2016; Towsey, Planitz, Nantes, Wimmer, & Roe, 2012). For instance, Towsey et al. (2012) were able to successfully detect the characteristic “whip-crack” of the eastern whipbird, *Psophodes olivaceus* (100% recall; 67% precision; 82% accuracy) using syntactic pattern recognition. For the frequency-modulated whistle of the currawong, *Strepera graculina*, they used hidden Markov models (40% recall; 100% precision; 90% accuracy), while for the pulsatile bellows of male koalas, they used binary template matching (75% recall; 75% precision; 95% accuracy). Recognizer performance is also affected by the distance of the calling individual from the sound recorder, given loss of amplitude as well as attenuation of high frequency sound components (Digby, Towsey, Bell, & Teal, 2013; Heinicke et al., 2015; Sebastián-González et al., 2015). Species that call in the infrasonic (very low frequency) and ultrasonic (very high frequency) ranges should have less acoustic overlap with other species, which may assist recognition. Indeed, Zeppelzauer, Hensman, and Stoeger (2015) reported an accuracy of 88.2% and a false positive rate of 13.7% for detecting the low-frequency rumbles of the African elephant. Their method involved signal enhancement to reduce the masking effects of low frequency noise, particularly wind and rain, which can be problematic for detecting infrasonic vocalizations. Ultrasonic vocalizations are less subject to the masking effects of noise, however, reviews of commercially available bat call detection software suggest poor reliability (Lemen, Freeman, White, & Andersen, 2015; Russo & Voigt, 2016).

Importantly, recognizer development must consider the vocal variability within and between individuals, social groups, and populations. If the species being monitored has a large repertoire, researchers or practitioners using bioacoustic methods should determine which vocalizations are of most use considering the program’s aims, and tailor the recognizer towards these. If vocalizations are highly variable, training data must properly represent this variability, such as by using calls from several individuals or groups. This includes the often-variable calls of juveniles (Priyadarshani et al., 2018). Notwithstanding, another challenge may be vocal instability, whereby individuals’ vocalizations vary over time, either through drift or vocal learning. The latter is particularly problematic for species that maintain the ability to learn vocalizations throughout life (open-ended vocal learning). For example, the vocalizations of palm cockatoos, while individually distinct, are thought to change over time (Zdenek, Heinsohn, & Langmore, 2018). Indeed, lifelong vocal learning is common in parrots (Bradbury & Balsby, 2016), and this should be considered in defining how similar a call must be to the recognizer for it to be detected.

In this regard, recognizer development is inherently about trade-offs; a highly specific recognizer may return few false positive detections but more false negatives, while a less specific recognizer will return more detections, but many may be false positives. For conservation programs aiming to detect rare or cryptic species or behaviors, specificity should be low. In such cases, manual verification will most likely be necessary, the time commitments for which must be considered (Cragg et al., 2015; Rocha, Ferreira, Paula, Rodrigues, & Sousa-Lima, 2015). Conversely, for programs in which detecting every call is not necessary, or where the cessation of a vocal behavior is of interest (e.g., to indicate the end of breeding), then reducing false positives by increasing specificity will be more important. For this reason, recognizers should ideally be built to align with the project’s aims (Priyadarshani et al., 2018), or should be easily altered as needs be. An example of this is the new template-matching R package *monitoR* (Hafner & Katz, 2017; Katz, Hafner, & Donovan, 2016) which allows the detection threshold (specificity) to be set by the end-user. Moreover, packages like *monitoR*, as well as other commercial software, assist enormously in making recognizer development accessible to the non-expert (i.e., people without expert programming skills), which is crucial if bioacoustics is to become widely applied in threatened species monitoring (Priyadarshani et al., 2018; Sebastián-González et al., 2015).

### 4 | CONCLUSION

The discipline of conservation behavior is still young, having only gained momentum over the last two decades. Except for the effects of anthropogenic noise (Shannon et al., 2016), monitoring of animal vocalizations has rarely been considered for its conservation implications, much less applied to solutions. Given the functions and behavioral contexts indicated by many vocalizations, however, we argue that bioacoustics can aid conservation and monitoring by providing an alternate means to capture individual- and group-level data. In particular, if vocal behaviors can inform decision-making as it relates to habitat management, then the potential for conservation achievement is substantial.

The specific acoustic signals monitored will vary according to the species and the problem at hand. For many threatened species, for which breeding success is often compromised, this requires that vocalizations reveal the
environmental factors that influence reproduction. For some, sufficient information may be gathered by monitoring discrete reproductive events, such as copulations or births. For others, more complex programs that monitor populations' social interactions, distress, movements or culture may be more informative. Before a monitoring program commences, however, it is important that a species' vocal behaviors are understood for the conservation-relevant data that they can provide. Unfortunately, for some less-studied species, this level of detail does not exist. In these cases, managers must decide whether to invest in acquiring that knowledge, or whether the mere occurrence of certain vocalizations that are already described, or exist in publicly available repositories (e.g., Macaulay Library, Cornell Lab of Ornithology, 2019), can be sufficiently informative (Table S1). Nonetheless, even if a species' repertoire is not fully described, bioacoustic programs can provide such information while monitoring is underway. Programs can later be adjusted, or acoustic data re-analyzed, to obtain additional behavioral information, if necessary.

Bioacoustics remains limited by the methods and technologies available to handle and process sound data. There are several dimensions to this problem and addressing them, we believe, will be critical to the widespread uptake and applicability of bioacoustics to conservation monitoring. Firstly, building call-classification recognizers often requires expert programming skills, which may limit the use of bioacoustics by ecologists or managers. To address this, collaboration with computer scientists and programmers should be encouraged. Commercial software that provides a user-friendly platform for non-experts to build recognizers must be used with caution (Russo & Voigt, 2016) and its limitations clearly articulated. Secondly, the computing power required to process sound files must be carefully considered. Bioacoustics can obtain excessive volumes of data, the processing of which can limit its efficiency. Lastly, and most importantly, any reporting of bioacoustic monitoring where a recognizer is used should include information on how the recognizer was constructed (i.e., the algorithm used; input data used) and statistics on recognizer performance. This should include both precision (number of true positive detections divided by the sum of true positive and false positive detections) and recall (number of true positive detections divided by the sum of true positive and false negative detections) (Towsey et al., 2012). This can be done at various levels, such as the individual call, the sound file, or the date of recording, depending on the program's aims. For example, a false negative detection could be defined as a species' presence being missed at a site on a given day and not an individual call being missed. To this end, the definitions of performance statistics, which have been used inconsistently in the literature, should also be provided.

In this study, we suggest that the overlap of three disciplines—vocal behavior, conservation behavior, and bioacoustics—can benefit threatened species monitoring. In essence, bioacoustics can help to define and monitor the behaviors that enable a species' persistence and recovery, and the environments in which these are supported. With a clear conservation direction, monitoring programs should consider the data that species' vocal behaviors can provide, as well as the relative costs of recording and analyzing them. Considering the variety of behaviors that are indicated by vocalizations, and their often pivotal role in fitness, the potential for bioacoustic monitoring of behavior to support conservation is likely to be substantial.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
D.T., M.M., and B.J.V.R. conceived the paper. D.T. wrote the paper with input from M.M. and B.J.V.R.

DATA ACCESSIBILITY STATEMENT
Data for Table S1 were accessed from the Macaulay Library at the Cornell Lab of Ornithology.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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