

Approaching wildlife with drones: using scientific literature to identify factors to consider for minimising disturbance

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ABSTRACT

Drones are a modern alternative to manned aircraft for aerial surveys, however approaching wildlife with drones may still cause disturbance. Understanding the factors influencing animal responses to drone flights is fundamental for informing guidance on lowest-impact flight practices. We reviewed scientific literature on drone flights conducted to approach wildlife and collated and quantified references to factors that should be considered in the development of guidelines and policies. The most referenced controllable factors were approach distance, noise emissions and airspeed. Other frequently referenced controllable factors included drone type, take-off distance, flight pattern, pilot experience and competence, whether consecutive flights were conducted and flight duration. The most referenced environmental factors were animal taxa, biological state of animals and ambient noise, followed by whether conspecifics are present, weather variables, habitat variables, whether animals have received previous exposure to anthropogenic settings, animals' behaviour prior to drone flights and whether predators are present. Policies and protocols that address these factors have an increased probability of minimising disturbance of drone flights. The variability in animal responses across different taxa, different ways drone flights are performed and the different circumstances they are deployed in highlights the need for taxa-specific protocols that also account for geographical and biological variations.

Key words: anthropogenic stimuli, behavioural reactions, policy considerations, unmanned aerial vehicles

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Introduction

In wildlife and land management, aerial surveillance is an important tool for covering distances and reaching remote and inaccessible locations that would be impossible using ground-based methods (Christie *et al.* 2016). Aerial surveys using manned aircraft have been applied to monitoring wildlife populations (Verfuss *et al.* 2019), habitat condition (Kim *et al.* 2018) and damage (Michez *et al.* 2016), as well as other conservation initiatives such as landscape-wide distributions of poisoned baits for invasive species (Johnston *et al.* 2016) and artificial food for threatened species (Mo *et al.* 2021). The advent of remotely piloted aircraft or unmanned aerial vehicles has overcome some of the limitations of manned aircraft, being superior in compactness, ease of deployment and saving financial costs and personnel time, as well as eliminating the risk of human mortality in the event of aircraft collisions (Chabot and Bird 2012; Anderson and Galston 2013).

In the past few decades, lightweight unmanned aerial vehicles weighing less than 30 kg have been developed (Hassanalian and Abdelkefi 2017). Herein referred to as drones (Chapman 2014), they have been applied

to a broad spectrum of purposes including defence and law enforcement (Reid 2014; Floreano and Wood 2014), agricultural practices (Frankelius *et al.* 2019), traffic monitoring (Coifman *et al.* 2006), surveying land (Tripicchio *et al.* 2015), disaster management (Restas 2015) and videography (Cheng 2015), as well as leisure activities by hobbyists and recreationalists (Siyuan 2015). However, use of drones for civilian purposes has brought challenges such as potential impacts on traditional notions of public safety, security, privacy, liability and ownership (Clothier *et al.* 2015; Rao *et al.* 2016), impacts on wildlife (Rebolo-Ifrán *et al.* 2019) and the need for regulation (Clarke and Moses 2014).

Anthropogenic disturbance to wildlife is an important concern for land managers, researchers, communities and government agencies (Gruas *et al.* 2020; Marion *et al.* 2020). Disturbance of animals is often considered as any human activity that alters their behaviour or physiology. Disturbance may impact animals at an individual level from energy expenditure from increased vigilance and fleeing responses (Houston *et al.* 2012), associated effects

on fitness and body condition (Creel *et al.* 2002), and influences on survival, fecundity and parental investment (Gill *et al.* 2001; Frid and Dill 2002). Disturbances over extended periods of time or broad spaces may carry effects over to species populations and local distributions (Marion *et al.* 2020). There is therefore a critical need to better understand these dynamics and develop management frameworks for addressing risks. Aerial surveys using manned aircraft expose target and non-target animals to disturbances such as noise emissions and downdrafts (Chabot and Bird 2012; Sardà-Palomera *et al.* 2012). In particular, sharing airspace between aircraft and volant wildlife such as birds and bats has a long history of management (Sodhi 2002; Blackwell *et al.* 2012). Although drones are notably less intrusive than manned aircraft, there remains potential disturbances to wildlife (Mulero-Pázmány *et al.* 2017).

A number of research studies have investigated the effects of drone flights on wildlife, which have highlighted variation in animal responses between taxa and other context factors (Smith *et al.* 2016; Mustafa *et al.* 2018). Peer-reviewed publications on ethical considerations (Vas *et al.* 2015) and best practice guidelines for approaching wildlife with drones (Hodgson and Koh 2016; Gonzalez and Johnson 2017) have been published. Understanding the factors influencing wildlife disturbances during drone flights is a fundamental step for informing the development of further policies (Lyons *et al.* 2018; Ramos *et al.* 2018; Wallace *et al.* 2018). Comprehensive reviews have synthesised the growing body of research on this subject matter (Chabot and Bird 2015; Christie *et al.* 2016; Colefax *et al.* 2018), however the factors that need to be considered would depend on the taxonomic and geographical scope of policies being developed. In this paper, we examined scientific literature reporting on practices involving approaching wildlife with drones to (1) collate factors that should be considered when developing guidelines and policies for drone flights around wildlife, (2) quantify the frequency of publications referring to each factor and (3) synthesise available information on these factors from publications.

Methods

We undertook a search for scientific literature that provided description or commentary of practices involving approaching wildlife with drones. In the search, we applied the keywords 'drone', 'unmanned aerial vehicle', 'unmanned aerial system', 'remotely-piloted aircraft system', 'unmanned aircraft', 'UAV', 'UAS' and 'RPAS' combined with 'wildlife', 'animals', 'birds', 'mammals', 'reptiles', 'amphibians', 'fish' and 'vertebrate' in Google Scholar. Scientific publications included peer-reviewed journal articles, university dissertations (including Masters theses), conference proceedings and project reports. We also identified additional publications from citations in other publications. Because our focus was on drone flights approaching animals, we excluded publications limited

to describing using drones in radiotelemetry or locating indirect signs of wildlife (e.g. nests). The search concluded on 28 January 2021.

Publications from our search were examined for factors involved in drone flight practices that would potentially influence animals' responses to drone flights, such as approach distance (the proximity between drones and animals) and airspeed. Factors that are directly manipulatable by drone pilots, such as drone characteristics or how drones are flown, were classed as 'controllable factors'. Factors relating to external variables not controllable by drone pilots such as the biology of animals and weather variables were classed as 'environmental factors'. We collated the factors noted in each publication to quantify the number of publications referencing each factor. It was not always immediately clear whether some practices noted in research studies were specifically purposed as controls to minimise wildlife disturbance. Some studies noted airspeed and time of day for their drone flights but not necessarily as considerations for minimising negative reactions to drone flights in animals; thus we exercised some interpretation to determine whether to record these factors against those publications. We recognise that these interpretations potentially lead to some inherent bias between factors. Research findings from studies that investigated animal responses to various controllable and environmental factors in drone flights were also recorded and synthesised for this review.

Results

We found 200 publications that provided description or commentary of flight practices of drones approaching wildlife, 178 peer-reviewed journal articles, eight project reports, seven university dissertations and seven conference proceedings (Fig. 1). Of these, 180 publications were concerning one or more specific taxonomical groups, being mammals (n=94), birds (n=82), reptiles (n=17) and fish (n=18). Research studies investigating animal responses to drone flights comprised 42 of publications, while 134 other publications were studies whose methodologies required approaching animals with drones. The remaining publications were either review papers, commentaries or protocols published in peer-reviewed journals.

Our review identified 182 publications that referenced controllable or environmental factors (the remaining publications are shown in the Appendix). Controllable factors were referenced in 180 publications (Table 1), and environmental factors were referenced in 86 publications (Table 2).

Interpretations of animal responses to drone flights

In most publications, animal responses to drone flights were assessed visually based on observations of behaviours. Behaviours interpreted as negative reactions included

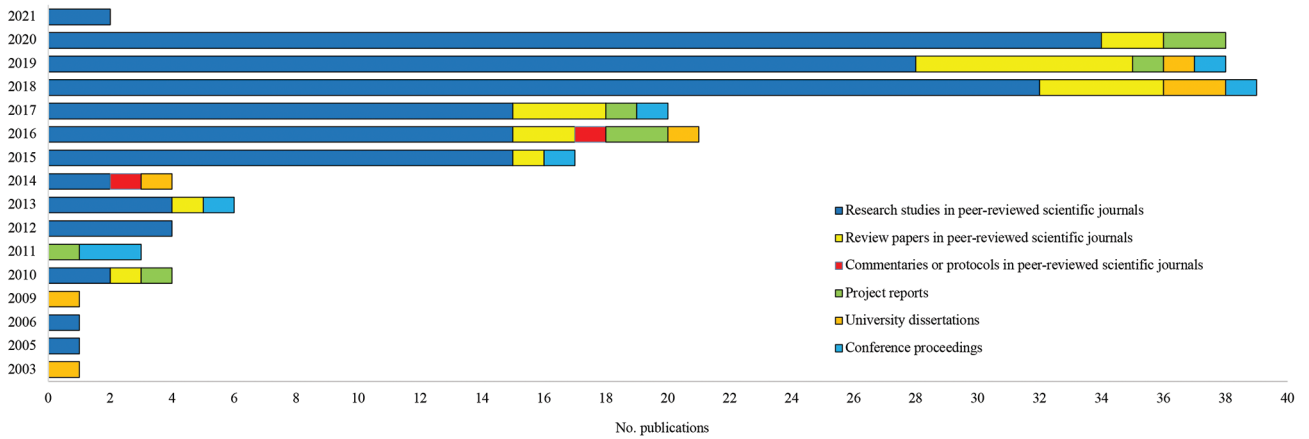


Fig. 1. Breakdown of scientific publications that provide description or commentary of flight practices of drones approaching wildlife arranged by publication type and year of publication.

Table I. Controllable factors referenced in scientific publications that potentially influence animal responses to drone flights.

Factor	No. publications	Citing publications
Pilot experience and competence	34	Jones <i>et al.</i> 2006; Chabot 2009, 2014; Mulero-Pázmány <i>et al.</i> 2014, 2017; Drever <i>et al.</i> 2015; Goebel <i>et al.</i> 2015; Junda <i>et al.</i> 2015; Christiansen <i>et al.</i> 2016a,b; Hodgson and Koh 2016; McClelland <i>et al.</i> 2016; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Gonzalez and Johnson 2017; Han <i>et al.</i> 2017; Pirota <i>et al.</i> 2017; Domínguez-Sánchez <i>et al.</i> 2018; Gooday <i>et al.</i> 2018; McIntosh <i>et al.</i> 2018; Mustafa <i>et al.</i> 2018; Torres <i>et al.</i> 2018; Wallace <i>et al.</i> 2018; Zmarz <i>et al.</i> 2018; Blight <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Lyons <i>et al.</i> 2019b; Raudino <i>et al.</i> 2019; Sorrell <i>et al.</i> 2019; Adams <i>et al.</i> 2020; Barr <i>et al.</i> 2020; DiGiacomo <i>et al.</i> 2020; Hyun <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Semel <i>et al.</i> 2020
Drone type	61	Perryman <i>et al.</i> 2014; Chabot and Bird 2015; Ditmer <i>et al.</i> 2015; Dulava <i>et al.</i> 2015; Goebel <i>et al.</i> 2015; Koski <i>et al.</i> 2015; Pomeroy <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Christiansen <i>et al.</i> 2016b; Christie <i>et al.</i> 2016; Hodgson and Koh 2016; Kidawa <i>et al.</i> 2016; Marine Mammal Commission 2016; McEvoy <i>et al.</i> 2016; Rümmler <i>et al.</i> 2016, 2018; Scobie and Hugenholtz 2016; Smith <i>et al.</i> 2016; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Fiori <i>et al.</i> 2017; Gonzalez and Johnson 2017; Hahn <i>et al.</i> 2017; Han <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Mustafa <i>et al.</i> 2017, 2018; Albores-Barajas <i>et al.</i> 2018; Arona <i>et al.</i> 2018; Barnas <i>et al.</i> 2018a; Bevan <i>et al.</i> 2018; Domínguez-Sánchez <i>et al.</i> 2018; Egan 2018; Lyons <i>et al.</i> 2018; McIntosh <i>et al.</i> 2018; Ramos <i>et al.</i> 2018; Rees <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Thompson <i>et al.</i> 2018; Torres <i>et al.</i> 2018; Valle and Scarton 2018, 2019; Zmarz <i>et al.</i> 2018; Barnas 2019; Bennitt <i>et al.</i> 2019; Brunton <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Johnston 2019; Pfeifer <i>et al.</i> 2019, 2021; Rebolo-Ifrán <i>et al.</i> 2019; Verfuss <i>et al.</i> 2019; Wandrie <i>et al.</i> 2019; Hyun <i>et al.</i> 2020; Mapes <i>et al.</i> 2020; Mesquita <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Rexer-Huber and Parker 2020; Weston <i>et al.</i> 2020; Dundas <i>et al.</i> 2021
Shape	28	Koski <i>et al.</i> 2015; Hodgson and Koh 2016; McEvoy <i>et al.</i> 2016; Rümmler <i>et al.</i> 2016, 2018; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Arona <i>et al.</i> 2018; Barnas <i>et al.</i> 2018a; Egan 2018; McIntosh <i>et al.</i> 2018; Mustafa <i>et al.</i> 2018; Rees <i>et al.</i> 2018; Thompson <i>et al.</i> 2018; Barnas 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Johnston 2019; Pfeifer <i>et al.</i> 2019, 2021; Wandrie <i>et al.</i> 2019; Mapes <i>et al.</i> 2020; Mesquita <i>et al.</i> 2020; Raoult <i>et al.</i> 2020
Size	25	Chabot and Bird 2015; Dulava <i>et al.</i> 2015; McEvoy <i>et al.</i> 2016; Smith <i>et al.</i> 2016; Borrelle and Fletcher 2017; Mulero-Pázmány <i>et al.</i> 2017; Rümmler <i>et al.</i> 2016, 2018; Mustafa <i>et al.</i> 2017, 2018; Albores-Barajas <i>et al.</i> 2018; Arona <i>et al.</i> 2018; Barnas <i>et al.</i> 2018a; Barnas <i>et al.</i> 2018a; McIntosh <i>et al.</i> 2018; Mustafa <i>et al.</i> 2018; Valle and Scarton 2018, 2019; Barnas 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Verfuss <i>et al.</i> 2019; Wandrie <i>et al.</i> 2019; Mesquita <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Rexer-Huber and Parker 2020; Weston <i>et al.</i> 2020
Colour	12	Chabot and Bird 2015; Vas <i>et al.</i> 2015; Hodgson and Koh 2016; Smith <i>et al.</i> 2016; Borrelle and Fletcher 2017; Albores-Barajas <i>et al.</i> 2018; Egan 2018; Rümmler <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Harris <i>et al.</i> 2019; Mapes <i>et al.</i> 2020; Dundas <i>et al.</i> 2021
Lights	2	Hahn <i>et al.</i> 2017; Albores-Barajas <i>et al.</i> 2018
Noise emissions	81	Jones 2003; Jones <i>et al.</i> 2006; Chabot 2009; Selby <i>et al.</i> 2011; Chabot and Bird 2015; Dulava <i>et al.</i> 2015; Durban <i>et al.</i> 2015; Goebel <i>et al.</i> 2015; Koski <i>et al.</i> 2015; Liu <i>et al.</i> 2015; Pomeroy <i>et al.</i> 2015; Allport 2016; Christiansen <i>et al.</i> 2016b, 2020; Christie <i>et al.</i> 2016; Hodgson and Koh 2016; Junda <i>et al.</i> 2016; Kidawa <i>et al.</i> 2016; Marine Mammal Commission 2016; McClelland <i>et al.</i> 2016; McEvoy <i>et al.</i> 2016; Rümmler <i>et al.</i> 2016, 2018; Scobie and Hugenholtz 2016; Smith <i>et al.</i> 2016; Sweeney <i>et al.</i> 2016; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Erbe <i>et al.</i> 2017; Fiori <i>et al.</i> 2017; Gonzalez and Johnson 2017; Hahn <i>et al.</i> 2017; Han <i>et al.</i> 2017; Johnston <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017, 2019; Mustafa <i>et al.</i> 2017, 2018; Pirota <i>et al.</i> 2017; Radiansyah <i>et al.</i> 2017; Wilson <i>et al.</i> 2017; Albores-Barajas <i>et al.</i> 2018; Aniceto <i>et al.</i> 2018; Arona <i>et al.</i> 2018; Barnas <i>et al.</i> 2018a,b; Bevan <i>et al.</i> 2018; Egan 2018; Howard <i>et al.</i> 2018; Lyons <i>et al.</i> 2018; McIntosh <i>et al.</i> 2018; Racanelli <i>et al.</i> 2018; Raoult <i>et al.</i> 2018; Rees <i>et al.</i> 2018; Thapa <i>et al.</i> 2018; Thompson <i>et al.</i> 2018; Valle and Scarton 2018, 2019; Wallace <i>et al.</i> 2018; Zmarz <i>et al.</i> 2018; Barnas 2019; Bennitt <i>et al.</i> 2019; Brunton <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i>

Factor	No. publications	Citing publications
Noise emissions (continued)	81	2019; Inman <i>et al.</i> 2019; Inoue <i>et al.</i> 2019; Johnston 2019; Kays <i>et al.</i> 2019; Pfeifer <i>et al.</i> 2019; Spaan <i>et al.</i> 2019; Verfuss <i>et al.</i> 2019; Wandrie <i>et al.</i> 2019; Adams <i>et al.</i> 2020; Centelleghé <i>et al.</i> 2020; Ditmer <i>et al.</i> 2020; Mapes <i>et al.</i> 2020; Mesquita <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Rischette <i>et al.</i> 2020; Weston <i>et al.</i> 2020
Changes in noise intensity	6	Sweeney <i>et al.</i> 2016; Mulero-Pázmány <i>et al.</i> 2017; Mustafa <i>et al.</i> 2018; Rümmler <i>et al.</i> 2018; Raoult <i>et al.</i> 2020; Rischette <i>et al.</i> 2020
Approach distance	170	Jones 2003; Jones <i>et al.</i> 2006; Chabot 2009, 2014; Acevedo-Whitehouse <i>et al.</i> 2010; Gardner <i>et al.</i> 2010; Israel 2011; Chabot and Bird 2012, 2015; Sardà-Palomera <i>et al.</i> 2012, 2017; Grenzdörffer 2013; A. Hodgson <i>et al.</i> 2013, 2017; Koski <i>et al.</i> 2013, 2015; Vermeulen <i>et al.</i> 2013; Barasona <i>et al.</i> 2014; King <i>et al.</i> 2014; Mulero-Pázmány <i>et al.</i> 2014, 2017; Perryman <i>et al.</i> 2014; Bevan <i>et al.</i> 2015, 2016, 2018; Chabot <i>et al.</i> 2015, 2019; Chrétien <i>et al.</i> 2015, 2016; Ditmer <i>et al.</i> 2015, 2020; Drever <i>et al.</i> 2015; Dulava <i>et al.</i> 2015; Durban <i>et al.</i> 2015; Goebel <i>et al.</i> 2015; Junda <i>et al.</i> 2015, 2016; Liu <i>et al.</i> 2015; Moreland <i>et al.</i> 2015; Pomeroy <i>et al.</i> 2015; Ratcliffe <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Weissensteiner <i>et al.</i> 2015; Bierlich and Johnston 2016; Brands 2016; Christiansen <i>et al.</i> 2016a,b, 2020; Christie <i>et al.</i> 2016; Gonzalez <i>et al.</i> 2016; J. Hodgson <i>et al.</i> 2016; Kidawa <i>et al.</i> 2016; Kiszka <i>et al.</i> 2016; Marine Mammal Commission 2016; McClelland <i>et al.</i> 2016; McEvoy <i>et al.</i> 2016; Rümmler <i>et al.</i> 2016, 2018; Scobie and Hugenholtz 2016; Smith <i>et al.</i> 2016; Sweeney <i>et al.</i> 2016; Adame <i>et al.</i> 2017; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Erbe <i>et al.</i> 2017; Fiori <i>et al.</i> 2017; Hahn <i>et al.</i> 2017; Johnston <i>et al.</i> 2017; Krause <i>et al.</i> 2017; Mustafa <i>et al.</i> 2017, 2018, 2019; Pirota <i>et al.</i> 2017; Radiansyah <i>et al.</i> 2017; Schofield <i>et al.</i> 2017; Sykora-Bodie <i>et al.</i> 2017; Wilson <i>et al.</i> 2017; Afán <i>et al.</i> 2018; Albores-Barajas <i>et al.</i> 2018; Angliss <i>et al.</i> 2018; Aniceto <i>et al.</i> 2018; Arona <i>et al.</i> 2018; Barnas <i>et al.</i> 2018a,b; Domínguez-Sánchez <i>et al.</i> 2018; Egan 2018; Ezat <i>et al.</i> 2018; Ferguson <i>et al.</i> 2018; Gentle <i>et al.</i> 2018; Hensel <i>et al.</i> 2018; Howard <i>et al.</i> 2018; Lea <i>et al.</i> 2018; Lyons <i>et al.</i> 2018, 2019a,b; McIntosh <i>et al.</i> 2018; Racanelli <i>et al.</i> 2018; Ramos <i>et al.</i> 2018; Raoult <i>et al.</i> 2018, 2020; Rieucou <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Su <i>et al.</i> 2018; Thapa <i>et al.</i> 2018; Thompson <i>et al.</i> 2018; Torres <i>et al.</i> 2018; Valle and Scarton 2018, 2019, 2020; Wallace <i>et al.</i> 2018; Weimerskirch <i>et al.</i> 2018; Witczuk <i>et al.</i> 2018; Zmarz <i>et al.</i> 2018; Allan <i>et al.</i> 2019; Barnas 2019; Bennitt <i>et al.</i> 2019; Blight <i>et al.</i> 2019; Bröker <i>et al.</i> 2019; Brunton <i>et al.</i> 2019, 2020; Burke <i>et al.</i> 2019a,b; Bushaw <i>et al.</i> 2019; Corcoran <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Hong <i>et al.</i> 2019; Horton <i>et al.</i> 2019; Inman <i>et al.</i> 2019; Inoue <i>et al.</i> 2019; Ireland <i>et al.</i> 2019; Johnston 2019; Kays <i>et al.</i> 2019; Korczak-Abshire <i>et al.</i> 2019; Lee <i>et al.</i> 2019; Magness <i>et al.</i> 2019; Pfeifer <i>et al.</i> 2019, 2021; Raudino <i>et al.</i> 2019; Rebololo-Ifrán <i>et al.</i> 2019; Sorrell <i>et al.</i> 2019; Spaan <i>et al.</i> 2019; Wandrie <i>et al.</i> 2019; Wang <i>et al.</i> 2019; Adams <i>et al.</i> 2020; Barr <i>et al.</i> 2020; Beaver <i>et al.</i> 2020; Bech-Hansen <i>et al.</i> 2020; Bird <i>et al.</i> 2020; Centelleghé <i>et al.</i> 2020; Hamilton <i>et al.</i> 2020; Hyun <i>et al.</i> 2020; Jarrett <i>et al.</i> 2020; Jech <i>et al.</i> 2020; Kelaher <i>et al.</i> 2020a,b; Mapes <i>et al.</i> 2020; McKellar <i>et al.</i> 2020; Mesquita <i>et al.</i> 2020; Oliveira-da-Costa <i>et al.</i> 2020; Oosthuizen <i>et al.</i> 2020; Parker and Rexer-Huber 2020; Porter <i>et al.</i> 2020; Rexer-Huber and Parker 2020; Rischette <i>et al.</i> 2020; Schroeder <i>et al.</i> 2020; Semel <i>et al.</i> 2020; Weston <i>et al.</i> 2020; Beranek <i>et al.</i> 2021; Dundas <i>et al.</i> 2021; Giles <i>et al.</i> 2021
Take-off distance	49	Chabot 2009; Gardner <i>et al.</i> 2010; Sardà-Palomera <i>et al.</i> 2012; Vas <i>et al.</i> 2015; Christiansen <i>et al.</i> 2016a; Hodgson <i>et al.</i> 2016; Kidawa <i>et al.</i> 2016; McEvoy <i>et al.</i> 2016; Rümmler <i>et al.</i> 2016, 2018; Smith <i>et al.</i> 2016; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Gonzalez and Johnson 2017; Mustafa <i>et al.</i> 2017, 2018; Radiansyah <i>et al.</i> 2017; Barnas <i>et al.</i> 2018a; Egan 2018; Ezat <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Thompson <i>et al.</i> 2018; Valle and Scarton 2018, 2019, 2020; Weimerskirch <i>et al.</i> 2018; Barnas 2019; Brunton <i>et al.</i> 2019, 2020; Chabot <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Inman <i>et al.</i> 2019; Inoue <i>et al.</i> 2019; Lee <i>et al.</i> 2019; Magness <i>et al.</i> 2019; Pfeifer <i>et al.</i> 2019; Spaan <i>et al.</i> 2019; Barr <i>et al.</i> 2020; Bech-Hansen <i>et al.</i> 2020; Bird <i>et al.</i> 2020; Jarrett <i>et al.</i> 2020; Mapes <i>et al.</i> 2020; Mesquita <i>et al.</i> 2020; Parker and Rexer-Huber 2020; Raoult <i>et al.</i> 2020; Rexer-Huber and Parker 2020; Rischette <i>et al.</i> 2020; Weston <i>et al.</i> 2020; Dundas <i>et al.</i> 2021
Flight pattern	58	Jones <i>et al.</i> 2006; Chabot and Bird 2015; Dulava <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Allport 2016; Christiansen <i>et al.</i> 2016b, 2020; Christie <i>et al.</i> 2016; Hodgson and Koh 2016; Kidawa <i>et al.</i> 2016; McClelland <i>et al.</i> 2016; McEvoy <i>et al.</i> 2016; Rümmler <i>et al.</i> 2016, 2018; Smith <i>et al.</i> 2016; Sweeney <i>et al.</i> 2016; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Gonzalez and Johnson 2017; Krause <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Mustafa <i>et al.</i> 2017, 2018; Wilson <i>et al.</i> 2017; Barnas <i>et al.</i> 2018a; Bevan <i>et al.</i> 2018; Egan 2018; Lyons <i>et al.</i> 2018; McIntosh <i>et al.</i> 2018; Ramos <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Torres <i>et al.</i> 2018; Valle and Scarton 2018, 2020; Wallace <i>et al.</i> 2018; Weimerskirch <i>et al.</i> 2018; Barnas 2019; Bennitt <i>et al.</i> 2019; Brunton <i>et al.</i> 2019, 2020; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; López and Mulero-Pázmány 2019; Spaan <i>et al.</i> 2019; Wandrie <i>et al.</i> 2019; Barr <i>et al.</i> 2020; Ditmer <i>et al.</i> 2020; Hyun <i>et al.</i> 2020; Jarrett <i>et al.</i> 2020; Mapes <i>et al.</i> 2020; Mesquita <i>et al.</i> 2020; Oosthuizen <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Rexer-Huber and Parker 2020; Rischette <i>et al.</i> 2020; Schroeder <i>et al.</i> 2020; Weston <i>et al.</i> 2020; Dundas <i>et al.</i> 2021
Angle of approach	52	Jones <i>et al.</i> 2006; Chabot and Bird 2015; Dulava <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Allport 2016; Christiansen <i>et al.</i> 2016b, 2020; Christie <i>et al.</i> 2016; Kidawa <i>et al.</i> 2016; McClelland <i>et al.</i> 2016; McEvoy <i>et al.</i> 2016; Rümmler <i>et al.</i> 2016, 2018; Smith <i>et al.</i> 2016; Sweeney <i>et al.</i> 2016; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Krause <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Mustafa <i>et al.</i> 2017, 2018; Wilson <i>et al.</i> 2017; Barnas <i>et al.</i> 2018a; Bevan <i>et al.</i> 2018; Egan 2018; Lyons <i>et al.</i> 2018; McIntosh <i>et al.</i> 2018; Ramos <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Torres <i>et al.</i> 2018; Valle and Scarton 2018, 2020; Wallace <i>et al.</i> 2018; Weimerskirch <i>et al.</i> 2018; Barnas 2019; Bennitt <i>et al.</i> 2019; Brunton <i>et al.</i> 2019; Wandrie <i>et al.</i> 2019; Barr <i>et al.</i> 2020; Ditmer <i>et al.</i> 2020; Hyun <i>et al.</i> 2020; Jarrett <i>et al.</i> 2020; Mapes <i>et al.</i> 2020; Mesquita <i>et al.</i> 2020; Oosthuizen <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Rexer-Huber and Parker 2020; Rischette <i>et al.</i> 2020; Schroeder <i>et al.</i> 2020; Weston <i>et al.</i> 2020; Dundas <i>et al.</i> 2021

Factor	No. publications	Citing publications
Airspeed	75	Jones 2003; Jones <i>et al.</i> 2006; Sardà-Palomera <i>et al.</i> 2012, 2017; Koski <i>et al.</i> 2013, 2015; Barasona <i>et al.</i> 2014; Chabot 2014; Chabot and Bird 2015; Chabot <i>et al.</i> 2015; Chrétien <i>et al.</i> 2015, 2016; Drever <i>et al.</i> 2015; Junda <i>et al.</i> 2015; Moreland <i>et al.</i> 2015; Ratcliffe <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Christie <i>et al.</i> 2016; Gonzalez <i>et al.</i> 2016; J. Hodgson <i>et al.</i> 2016; Kiszka <i>et al.</i> 2016; Marine Mammal Commission 2016; McClelland <i>et al.</i> 2016; McEvoy <i>et al.</i> 2016; Smith <i>et al.</i> 2016; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Erbe <i>et al.</i> 2017; A. Hodgson <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Mustafa <i>et al.</i> 2017, 2019; Radiansyah <i>et al.</i> 2017; Schofield <i>et al.</i> 2017; Afán <i>et al.</i> 2018; Albores-Barajas <i>et al.</i> 2018; Angliss <i>et al.</i> 2018; Bevan <i>et al.</i> 2018; Ferguson <i>et al.</i> 2018; Gentle <i>et al.</i> 2018; Hensel <i>et al.</i> 2018; Lyons <i>et al.</i> 2018, 2019a; McIntosh <i>et al.</i> 2018; Racanelli <i>et al.</i> 2018; Rümmler <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Thapa <i>et al.</i> 2018; Weimerskirch <i>et al.</i> 2018; Allan <i>et al.</i> 2019; Blight <i>et al.</i> 2019; Bröker <i>et al.</i> 2019; Corcoran <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Kays <i>et al.</i> 2019; Korczak-Abshire <i>et al.</i> 2019; Lee <i>et al.</i> 2019; Pfeifer <i>et al.</i> 2019; Sorrell <i>et al.</i> 2019; Valle and Scarton 2019, 2020; Wandrie <i>et al.</i> 2019; Barr <i>et al.</i> 2020; Beaver <i>et al.</i> 2020; Bird <i>et al.</i> 2020; Brunton <i>et al.</i> 2020; Hyun <i>et al.</i> 2020; Jarrett <i>et al.</i> 2020; Kelaher <i>et al.</i> 2020a,b; Mesquita <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Rexer-Huber and Parker 2020; Schroeder <i>et al.</i> 2020; Beranek <i>et al.</i> 2021; Dundas <i>et al.</i> 2021
Timing	47	Sardà-Palomera <i>et al.</i> 2012, 2017; Vermeulen <i>et al.</i> 2013; Chabot and Bird 2015; Junda <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Christie <i>et al.</i> 2016; Marine Mammal Commission 2016; Rümmler <i>et al.</i> 2016, 2018; Smith <i>et al.</i> 2016; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Fiori <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Mustafa <i>et al.</i> 2017, 2018; Radiansyah <i>et al.</i> 2017; Afán <i>et al.</i> 2018; Albores-Barajas <i>et al.</i> 2018; Barnas <i>et al.</i> 2018b; Bevan <i>et al.</i> 2018; Lyons <i>et al.</i> 2018, 2019b; Rush <i>et al.</i> 2018; Wallace <i>et al.</i> 2018; Weimerskirch <i>et al.</i> 2018; Barnas 2019; Bennitt <i>et al.</i> 2019; Brunton <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Kays <i>et al.</i> 2019; Lee <i>et al.</i> 2019; Spaan <i>et al.</i> 2019; Adams <i>et al.</i> 2020; Bech-Hansen <i>et al.</i> 2020; Centelleghé <i>et al.</i> 2020; Dittmer <i>et al.</i> 2020; Mapes <i>et al.</i> 2020; Oosthuizen <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Rexer-Huber and Parker 2020; Semel <i>et al.</i> 2020; Valle and Scarton 2020; Dundas <i>et al.</i> 2021; Giles <i>et al.</i> 2021
Flight duration	21	Junda <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Christie <i>et al.</i> 2016; Borrelle and Fletcher 2017; Fiori <i>et al.</i> 2017; Albores-Barajas <i>et al.</i> 2018; Barnas <i>et al.</i> 2018b; Mustafa <i>et al.</i> 2018; Wallace <i>et al.</i> 2018; Barnas 2019; Harris <i>et al.</i> 2019; Kays <i>et al.</i> 2019; Lee <i>et al.</i> 2019; Centelleghé <i>et al.</i> 2020; Dittmer <i>et al.</i> 2020; Oosthuizen <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Semel <i>et al.</i> 2020; Valle and Scarton 2020; Dundas <i>et al.</i> 2021; Giles <i>et al.</i> 2021
Frequency of flights	2	Borrelle and Fletcher 2017; Harris <i>et al.</i> 2019
Consecutive flights	23	Sardà-Palomera <i>et al.</i> 2012, 2017; Vermeulen <i>et al.</i> 2013; Chabot and Bird 2015; Christie <i>et al.</i> 2016; Rümmler <i>et al.</i> 2016, 2018; Smith <i>et al.</i> 2016; Brisson-Curadeau <i>et al.</i> 2017; Mustafa <i>et al.</i> 2017; Radiansyah <i>et al.</i> 2017; Ramos <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Brunton <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Lee <i>et al.</i> 2019; Spaan <i>et al.</i> 2019; Adams <i>et al.</i> 2020; Dittmer <i>et al.</i> 2020; Mapes <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Dundas <i>et al.</i> 2021
Intervals between consecutive flights	7	Sardà-Palomera <i>et al.</i> 2012; Vermeulen <i>et al.</i> 2013; Rümmler <i>et al.</i> 2016, 2018; Brisson-Curadeau <i>et al.</i> 2017; Radiansyah <i>et al.</i> 2017; Dittmer <i>et al.</i> 2020
Time of day	10	Mulero-Pázmány <i>et al.</i> 2017; Afán <i>et al.</i> 2018; Bevan <i>et al.</i> 2018; Lyons <i>et al.</i> 2018; Weimerskirch <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Kays <i>et al.</i> 2019; Rexer-Huber and Parker 2020
Time of year	10	Junda <i>et al.</i> 2015; Christie <i>et al.</i> 2016; Marine Mammal Commission 2016; Mustafa <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Brunton <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Lyons <i>et al.</i> 2018, 2019b; Bech-Hansen <i>et al.</i> 2020
Allowance of habituation periods	6	Bierlich and Johnston 2016; Rümmler <i>et al.</i> 2016; Egan 2018; Harris <i>et al.</i> 2019; Wandrie <i>et al.</i> 2019; Mapes <i>et al.</i> 2020
Geographic location	5	Pomeroy <i>et al.</i> 2015; Smith <i>et al.</i> 2016; Borrelle and Fletcher 2017; Mustafa <i>et al.</i> 2018; Giles <i>et al.</i> 2021

Table 2. Environmental factors referenced in scientific publications that potentially influence animal responses to drone flights.

Factor	No. publications	Citing publications
Taxa	58	Drever <i>et al.</i> 2015; Dulava <i>et al.</i> 2015; Pomeroy <i>et al.</i> 2015; Junda <i>et al.</i> 2016; Kidawa <i>et al.</i> 2016; Marine Mammal Commission 2016; Scobie and Hugenholtz 2016; Smith <i>et al.</i> 2016; Adame <i>et al.</i> 2017; Borrelle and Fletcher 2017; Brisson-Curadeau <i>et al.</i> 2017; Erbe <i>et al.</i> 2017; Fiori <i>et al.</i> 2017; Gonzalez and Johnson 2017; Mustafa <i>et al.</i> 2017, 2018; Albores-Barajas <i>et al.</i> 2018; Arona <i>et al.</i> 2018; Barnas <i>et al.</i> 2018a; Bevan <i>et al.</i> 2018; Domínguez-Sánchez <i>et al.</i> 2018; Egan 2018; Lyons <i>et al.</i> 2018, 2019b; McIntosh <i>et al.</i> 2018; Ramos <i>et al.</i> 2018; Raoult <i>et al.</i> 2018, 2020; Rees <i>et al.</i> 2018; Rümmler <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Thompson <i>et al.</i> 2018; Valle and Scarton 2018, 2019, 2020; Wallace <i>et al.</i> 2018; Weimerskirch <i>et al.</i> 2018; Barnas 2019; Bennitt <i>et al.</i> 2019; Brunton <i>et al.</i> 2019; Burke <i>et al.</i> 2019b; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Johnston 2019; Adams <i>et al.</i> 2020; Barr <i>et al.</i> 2020; Bech-Hansen <i>et al.</i> 2020; Jarrett <i>et al.</i> 2020; Lachman <i>et al.</i> 2020; Mapes <i>et al.</i> 2020; Mesquita <i>et al.</i> 2020; Rexer-Huber and Parker 2020; Rischette <i>et al.</i> 2020; Schroeder <i>et al.</i> 2020; Weston <i>et al.</i> 2020; Dundas <i>et al.</i> 2021; Giles <i>et al.</i> 2021; Pfeifer <i>et al.</i> 2021
Visual acuity	1	Mesquita <i>et al.</i> 2020
Auditory acuity	4	Scobie and Hugenholtz 2016; Erbe <i>et al.</i> 2017; Rees <i>et al.</i> 2018; Mapes <i>et al.</i> 2020
Presence of conspecifics	21	Dulava <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Hahn <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; McIntosh <i>et al.</i> 2018; Mustafa <i>et al.</i> 2018; Rümmler <i>et al.</i> 2018; Thapa <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Brunton <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Barr <i>et al.</i> 2020; Bech-Hansen <i>et al.</i> 2020; Jarrett <i>et al.</i> 2020; Mapes <i>et al.</i> 2020; Mesquita <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Schroeder <i>et al.</i> 2020; Valle and Scarton 2020; Dundas <i>et al.</i> 2021; Giles <i>et al.</i> 2021
Group size of animals	19	Dulava <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Mulero-Pázmány <i>et al.</i> 2017; McIntosh <i>et al.</i> 2018; Rümmler <i>et al.</i> 2018; Thapa <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Brunton <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Barr <i>et al.</i> 2020; Bech-Hansen <i>et al.</i> 2020; Jarrett <i>et al.</i> 2020; Mapes <i>et al.</i> 2020; Mesquita <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Schroeder <i>et al.</i> 2020; Valle and Scarton 2020; Dundas <i>et al.</i> 2021; Giles <i>et al.</i> 2021
Age	11	Kidawa <i>et al.</i> 2016; Smith <i>et al.</i> 2016; Fiori <i>et al.</i> 2017; Gonzalez and Johnson 2017; Arona <i>et al.</i> 2018; Bevan <i>et al.</i> 2018; Ramos <i>et al.</i> 2018; Weimerskirch <i>et al.</i> 2018; Mesquita <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Rexer-Huber and Parker 2020
Sex	3	Kidawa <i>et al.</i> 2016; Fiori <i>et al.</i> 2017; Bevan <i>et al.</i> 2018
Biological state	32	Dulava <i>et al.</i> 2015; Junda <i>et al.</i> 2015; Ratcliffe <i>et al.</i> 2015; Pomeroy <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Christie <i>et al.</i> 2016; Junda <i>et al.</i> 2016; Kidawa <i>et al.</i> 2016; Smith <i>et al.</i> 2016; Brisson-Curadeau <i>et al.</i> 2017; Fiori <i>et al.</i> 2017; Gonzalez and Johnson 2017; Johnston <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Bevan <i>et al.</i> 2018; Lyons <i>et al.</i> 2018, 2019b; Mustafa <i>et al.</i> 2018; Rümmler <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Thapa <i>et al.</i> 2018; Valle and Scarton 2018, 2019; Weimerskirch <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Johnston 2019; Lee <i>et al.</i> 2019; Mapes <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Beranek <i>et al.</i> 2021; Dundas <i>et al.</i> 2021
Breeding status	31	Dulava <i>et al.</i> 2015; Junda <i>et al.</i> 2015; Ratcliffe <i>et al.</i> 2015; Pomeroy <i>et al.</i> 2015; Vas <i>et al.</i> 2015; Christie <i>et al.</i> 2016; Junda <i>et al.</i> 2016; Kidawa <i>et al.</i> 2016; Smith <i>et al.</i> 2016; Brisson-Curadeau <i>et al.</i> 2017; Fiori <i>et al.</i> 2017; Gonzalez and Johnson 2017; Johnston <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Bevan <i>et al.</i> 2018; Lyons <i>et al.</i> 2018, 2019b; Mustafa <i>et al.</i> 2018; Rümmler <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Thapa <i>et al.</i> 2018; Valle and Scarton 2018, 2019; Weimerskirch <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Johnston 2019; Lee <i>et al.</i> 2019; Mapes <i>et al.</i> 2020; Beranek <i>et al.</i> 2021; Dundas <i>et al.</i> 2021
Moulting status	5	Pomeroy <i>et al.</i> 2015; Kidawa <i>et al.</i> 2016; Fiori <i>et al.</i> 2017; Johnston <i>et al.</i> 2017; Lee <i>et al.</i> 2019
Animal condition	3	Gonzalez and Johnson 2017; Rümmler <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019
Biochemical state	2	Rümmler <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019
Injury or sickness	1	Gonzalez and Johnson 2017
Exposure to anthropogenic settings	19	Dulava <i>et al.</i> 2015; Pomeroy <i>et al.</i> 2015; Allport 2016; Christie <i>et al.</i> 2016; Marine Mammal Commission 2016; Smith <i>et al.</i> 2016; Rümmler <i>et al.</i> 2018; Rush <i>et al.</i> 2018; Thompson <i>et al.</i> 2018; Blight <i>et al.</i> 2019; Brunton <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Horton <i>et al.</i> 2019; Inman <i>et al.</i> 2019; Raudino <i>et al.</i> 2019; Wandrie <i>et al.</i> 2019; Jarrett <i>et al.</i> 2020; Schroeder <i>et al.</i> 2020; Giles <i>et al.</i> 2021
Behavioural state	15	Potapov <i>et al.</i> 2013; Christie <i>et al.</i> 2016; Smith <i>et al.</i> 2016; Fiori <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Bevan <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Horton <i>et al.</i> 2019; Centelleghé <i>et al.</i> 2020; Jarrett <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Rexer-Huber and Parker 2020; Schroeder <i>et al.</i> 2020; Giles <i>et al.</i> 2021
Animals flying in airspace	2	Raoult <i>et al.</i> 2020; Rexer-Huber and Parker 2020

Factor	No. publications	Citing publications
Activity prior to drone flight	13	Potapov <i>et al.</i> 2013; Christie <i>et al.</i> 2016; Smith <i>et al.</i> 2016; Fiori <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Bevan <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Horton <i>et al.</i> 2019; Centelleghé <i>et al.</i> 2020; Jarrett <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Giles <i>et al.</i> 2021
Habitat variables	19	Ditmer <i>et al.</i> 2015; Allport 2016; Marine Mammal Commission 2016; Rümmler <i>et al.</i> 2016, 2018; Scobie and Hugenholtz 2016; Smith <i>et al.</i> 2016; Fiori <i>et al.</i> 2017; Mulero-Pázmány <i>et al.</i> 2017; Bevan <i>et al.</i> 2018; Domínguez-Sánchez <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Jarrett <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Semel <i>et al.</i> 2020; Schroeder <i>et al.</i> 2020; Giles <i>et al.</i> 2021
Geophysical environment	7	Marine Mammal Commission 2016; Rümmler <i>et al.</i> 2016, 2018; Bevan <i>et al.</i> 2018; Harris <i>et al.</i> 2019; Jarrett <i>et al.</i> 2020; Raoult <i>et al.</i> 2020
Vegetation type and density	6	Ditmer <i>et al.</i> 2015; Allport 2016; Scobie and Hugenholtz 2016; Smith <i>et al.</i> 2016; Bennitt <i>et al.</i> 2019; Jarrett <i>et al.</i> 2020
Water clarity	3	Bevan <i>et al.</i> 2018; Raoult <i>et al.</i> 2020; Giles <i>et al.</i> 2021
Weather variables	20	Ditmer <i>et al.</i> 2015; Goebel <i>et al.</i> 2015; Marine Mammal Commission 2016; Rümmler <i>et al.</i> 2016, 2018; Erbe <i>et al.</i> 2017; Fiori <i>et al.</i> 2017; Lyons <i>et al.</i> 2018; Mustafa <i>et al.</i> 2017, 2018; Ramos <i>et al.</i> 2018; Weimerskirch <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Mapes <i>et al.</i> 2020; Raoult <i>et al.</i> 2020; Rischette <i>et al.</i> 2020; Schroeder <i>et al.</i> 2020; Giles <i>et al.</i> 2021
Cloud cover	3	Fettermann <i>et al.</i> 2019; Mapes <i>et al.</i> 2020; Giles <i>et al.</i> 2021
Wind	15	Ditmer <i>et al.</i> 2015; Goebel <i>et al.</i> 2015; Rümmler <i>et al.</i> 2016; Fiori <i>et al.</i> 2017; Mustafa <i>et al.</i> 2017; Lyons <i>et al.</i> 2018; Ramos <i>et al.</i> 2018; Weimerskirch <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Raoult <i>et al.</i> 2020; Rischette <i>et al.</i> 2020; Schroeder <i>et al.</i> 2020; Giles <i>et al.</i> 2021
Sea state	5	Goebel <i>et al.</i> 2015; Fiori <i>et al.</i> 2017; Fettermann <i>et al.</i> 2019; Raoult <i>et al.</i> 2020; Giles <i>et al.</i> 2021
Ambient noise	22	Ditmer <i>et al.</i> 2015; Goebel <i>et al.</i> 2015; Christiansen <i>et al.</i> 2016b, 2020; Marine Mammal Commission 2016; Rümmler <i>et al.</i> 2016; Smith <i>et al.</i> 2016; Borrelle and Fletcher 2017; Erbe <i>et al.</i> 2017; Fiori <i>et al.</i> 2017; Johnston <i>et al.</i> 2017; Arona <i>et al.</i> 2018; Bevan <i>et al.</i> 2018; Lyons <i>et al.</i> 2018; McIntosh <i>et al.</i> 2018; Bennitt <i>et al.</i> 2019; Fettermann <i>et al.</i> 2019; Harris <i>et al.</i> 2019; Pfeifer <i>et al.</i> 2019; Verfuss <i>et al.</i> 2019; Mesquita <i>et al.</i> 2020; Raoult <i>et al.</i> 2020
Presence of predators	15	Junda <i>et al.</i> 2015; McEvoy <i>et al.</i> 2016; Rümmler <i>et al.</i> 2016, 2018; Brisson-Curadeau <i>et al.</i> 2017; Mustafa <i>et al.</i> 2017; Barnas <i>et al.</i> 2018a; Valle and Scarton 2018, 2019, 2020; Barnas 2019; Harris <i>et al.</i> 2019; Lyons <i>et al.</i> 2019b; Jarrett <i>et al.</i> 2020; Mapes <i>et al.</i> 2020
Exposure to other anthropogenic disturbances	7	Rümmler <i>et al.</i> 2016, 2018; Barnas <i>et al.</i> 2018a; Torres <i>et al.</i> 2018; Horton <i>et al.</i> 2019; Raoult <i>et al.</i> 2020; Giles <i>et al.</i> 2021

fleeing or flushing (e.g. Inoue *et al.* 2019; Bech-Hansen *et al.* 2020), alarm-calling (e.g. Albores-Barajas *et al.* 2018; Kay *et al.* 2019), ceasing pre-disturbance activities such as foraging (e.g. McEvoy *et al.* 2016; Radiansyah *et al.* 2017) and attacking (e.g. Junda *et al.* 2015, 2016; Lyons *et al.* 2018) or mobbing drones (e.g. Mesquita *et al.* 2020), as well as aquatic animals submerging (e.g. Bevan *et al.* 2018; Inman *et al.* 2019), arboreal animals descending to lower elevations (e.g. Kay *et al.* 2019) and cetaceans performing chin- or tail-slaps, spy-hop and side-float postures (e.g. Fettermann *et al.* 2019) and deep-diving (e.g. Giles *et al.* 2021). For stationary animals, their responses were often interpreted as not being disturbed if there were no observable movements (e.g. Oosthuizen *et al.* 2020). For animals in locomotion, responses were interpreted as negative reactions if there were observable changes to their activity patterns during drone flights (such as changes in speed or direction of movement; e.g. Christiansen *et al.* 2020), or no disturbance if activity patterns continued consistently as before drone flights commenced (e.g. Centelleghé *et al.* 2020).

Some studies applied systematic approaches to assessing animal responses, such as scaled matrices of behaviours representing proxies of different levels of responses (e.g. McEvoy *et al.* 2016; Rümmler *et al.* 2016; Rischette *et al.* 2020); for example, no observable reactions to drones were arranged at one end of the scale, behaviours clearly indicating disturbance (such as fleeing) at the other end of the scale, and vigilance behaviours (such as glancing at drones but not fleeing) arranged as intermediary levels of negative reactions. For colonial taxa, some studies considered levels of animal responses in terms of the proportion of individuals exhibiting negative reactions (e.g. McIntosh *et al.* 2018; Mesquita *et al.* 2020). We found 28 studies that deployed statistical models to differentiate animal activity patterns during drone flights and in the absence of drones (control). For instance, one study statistically compared disturbance scores prior to and during drone flights (Chabot *et al.* 2015). Some studies also measured time spent off nests or distances animals moved away from their original position, as well as whether nesting birds resumed brooding in the days following drone flights (e.g. Valle and Scarton 2019, 2020).

Five studies also applied physiological parameters to investigate animal responses, such as changes in heart rate (Ditmer *et al.* 2015, 2020; Domínguez-Sánchez *et al.* 2018; Howard *et al.* 2018; Weimerskirch *et al.* 2018). These studies identified stress responses in animals even when there were no visually observable changes in behaviour to indicate disturbance. Some studies measured interbreath intervals in cetaceans (between surfacing for air) as a proxy for respiration rates (e.g. Domínguez-Sánchez *et al.* 2018; Christiansen *et al.* 2020).

Controllable factors potentially influencing animal responses to drone flights

The most referenced controllable factor was approach distance (n=170), which is the distance drones are flown toward animals (Table 1). The next most referenced controllable factors were noise emissions from drones (n=81) and airspeed (n=75). We note that the large number of references to factors such as approach distance and airspeed were potentially due to these flight characteristics being fundamentally important details to report in the methodologies of journal articles based on research studies.

Approach distance

Approach distance was also termed separation distance in some publications, or flight height or vertical distance in reference to altitude. Research findings on animal responses to drones flown at specific approach distances were reported in 80 publications. The taxonomical groups covered by these studies spanned 22 orders of mammals, birds, reptiles and fish: Diprotodontia (n=2), Primates (n=5), Carnivora (n=13), Sirenia (n=2), Proboscidea (n=3), Artiodactyla (n=19), Perissodactyla (n=2), Podicipediformes (n=2), Anseriformes (n=6), Charadriiformes (n=19), Suliformes (n=4), Pelecaniformes (n=6), Ciconiiformes (n=1), Procellariiformes (n=2), Sphenisciformes (n=9), Apodiformes (n=1), Passeriformes (n=2), Galliformes (n=2), Accipitriformes (n=1), Testudines (n=3), Crocodylia (n=1), Carcharhiniformes (n=1). Across these studies, animal responses were consistently stronger at reduced approach distances. Research findings of drone flights eliciting no observable reactions in subject animals or only minor reactions (such as increased vigilance) above certain approach distances were found in 60 studies. However, some publications recognised that the effects of approach distances are influenced by other factors such as drone characteristics and environmental factors (Pomeroy *et al.* 2015; McIntosh *et al.* 2018).

Noise emissions

Of the 81 publications that referenced noise emissions, six also referenced sudden changes in noise intensity (Table 1). These changes in noise intensity were attributed to flight angles; for example, two publications noted greater noise emissions from their drone during vertical ascents

compared to horizontal passes (Mustafa *et al.* 2017; Weston *et al.* 2020), and Rischette *et al.* (2020) found that their drone was forced to increase its flight angle during high winds in order to maintain a linear flight path, during which higher noise emissions resulted.

Four publications stated that the audibility of drones decreases with increasing approach distance (Koski *et al.* 2015; Racanelli *et al.* 2018). The thresholds at which noise emissions become inaudible to human hearing were determined in two studies, being approach distances of 50 m in Weston *et al.* (2020) and 200 m in Liu *et al.* (2015). Studies of aquatic environments found that much of the sound energy from drones is reflected off the water surface, resulting in reduced noise levels underwater (Christiansen *et al.* 2016b, 2020; Erbe *et al.* 2017). Noise emissions can also be masked by ambient noise such as vocalisations from animal colonies, wind and moving water, possibly causing animals to not detect drones audibly (McIntosh *et al.* 2018; Christiansen *et al.* 2020; Mesquita *et al.* 2020). One study proposed that wind masking noise emissions may have contributed to disturbance to American Black Bears *Ursus americanus* when animals eventually perceived the drone approaching; rather than anticipating the approaching drone from afar, the bears were caught by surprise when they perceived the drone at close proximity (Ditmer *et al.* 2015). Only one publication reported possible differentiation between the effects of noise emissions and visual stimulus; Allport (2016) reported a drone being launched from behind thick vegetation and observed Whimbrels *Numenius phaeopus* exhibiting vigilance in response to noise emissions and not flushing until the drone appeared over the top of the vegetation.

Airspeed

Airspeed (or ground speed, flight speed or cruising speed in some publications) was the third most referenced controllable factor (Table 1). However, only two publications reported thresholds that elicited negative reactions from animals. First, Schroeder *et al.* (2020) found that while different airspeeds had no effect on Guanacos *Lama guanicoe* at close range, there was a higher likelihood of causing disturbance when their drone was further away travelling at 8-10 m per second compared to slower airspeeds. Second, Dundas *et al.* (2021) noticed less disturbance to waterfowl contrarily when their drone moved faster (5-7 m per second), speculating that faster airspeeds potentially reduce the probability of the birds detecting the drone. A further study of seabirds using different approach distances (40 m, 60m, 80m) and airspeeds (<62 m per second) found no differences in responses to different airspeeds (Rexer-Huber and Parker 2020).

There were some studies in which drones were flown at high airspeeds (up to 10-46 m per second) at high altitudes (91-305 m above ground level) (e.g. Chabot *et al.* 2015; Angliss *et al.* 2018; Bröker *et al.* 2019;

McKellar *et al.* 2020). In two of these studies, drone flights had no statistically significant effects on nesting seabird behaviours (Chabot 2014; Chabot *et al.* 2015; McKellar *et al.* 2020), which reflects how airspeed may be less important at greater approach distances in some contexts (c.f. Schroeder *et al.* 2020). Similarly, drones are less likely to be visually perceived by animals on the ground as approach distance is increased vertically (Chabot 2009; Racanelli *et al.* 2018).

Drone type and characteristics

Drone type was referenced as a controllable factor influencing animal responses in 61 publications (Table 1). Four studies specifically found variances in responses to different drone makes and models (Pomeroy *et al.* 2015; Kidawa *et al.* 2016; Scobie and Hugenholtz 2016; Egan 2018). The most referenced attributes of drone type were shape ($n=28$), size ($n=25$) and colour ($n=12$). Lights emitted from drones was only referenced in two publications.

Four publications that detailed the effects of drone shape on animal responses referenced how closely drones of particular outlines resembled aerial predators (Koski *et al.* 2015; Pfeifer *et al.* 2019). Two of these studies provided research findings validating these inferences. First, McEvoy *et al.* (2016) recorded higher amounts of flushing in waterfowl using a drone with a delta-wing design (resembling a bird of prey) compared to two other fixed-wing and two multirotor drone types flown at equivalent flight characteristics. Second, Egan (2018) specially modified a drone to resemble a bird of prey, which elicited negative reactions from Red-winged Blackbirds *Agelaius phoeniceus* at further approach distances compared to two commercially available drones (one also a fixed-wing drone and a multirotor drone).

Some publications suggested potential disturbance effects from drones casting silhouettes over colonies or individual animals. Silhouettes are a function of the shape and size of the drone, as well as cloud cover and time of day. Only one research study differentiated animal responses between drones of different sizes, finding that DJI Phantom 4 and DJI Phantom 4 Pro drones (35 cm diagonal size) elicited fewer negative reactions from Australian Fur Seals *Arctocephalus pusillus doriferus* and nesting Silver Gulls *Chroicocephalus novaehollandiae* than a Gryphon Dynamics X8-1400 drone (140 cm diagonal size). However, this study (McIntosh *et al.* 2018) also recognised that the smaller drones were quieter, which partially explains why they were flown at closer approach distances without causing animals to be alarmed.

Drone colour was referenced in 12 publications, but only one investigated the effects on animal responses; Mapes *et al.* (2020) observed Least Terns *Sternula antillarum*, Common Terns *S. hirundo* and Black Skimmers *Rynchops niger* flushing in response to approaches by their drone

in its original black colour and painted with a “dazzle camouflage” pattern, however equivalent approaches by a drone painted sky blue did not elicit any observable reactions from the birds. This study suggested that camouflaging the drone in blue paint made it more difficult for birds to perceive it visually against the colour of the sky. However, cloud cover appeared to reduce the effectiveness of this camouflage, casting drones of any colours as dark objects (Mapes *et al.* 2020). There may also be logistic difficulties to consider, such as camouflaged drones being more difficult for drone pilots and other observers to visually track, thus potentially leading to safety issues such as collisions with stationary objects or manned aircraft in the same airspace.

Take-off distance

Take-off distance refers to the distance separation between subject animals and the site drones are launched, intended as a buffer to any potential disturbance from take-off. Take-off distance was referenced in 49 publications (Table 1), a number of which recommended launching drones outside of animals’ field of view (e.g. Inman *et al.* 2019). Eight publications reported observations of the effects of take-off distances on animal responses, which consistently showed that greater take-off distances resulted in less disturbance during take-off. These findings were mainly limited to studies of waterbirds, aquatic birds and pinnipeds. However, one study on Red-winged Blackbirds found that launching drones from a further distance allowed drones to approach closer before blackbirds exhibited reactions (Egan 2018).

Flight pattern

The potential influence of flight pattern on animal responses was referenced in 58 publications (Table 1), the majority of which specifically referenced the potential influence of angles of approach ($n=52$). Most studies applied sweeping horizontal flight patterns at pre-determined survey altitudes to gather data, however drones were also described undertaking altitudinal movements (vertical descends or ascents) and diagonal movements towards animals (altitudinal changes during horizontal approach).

Nineteen studies reported observations of animal responses to specific angles of approach. Seven of them reported drones performing vertical descends eliciting stronger reactions than horizontal overhead flights in penguins (Rümmler *et al.* 2016, 2018; Mustafa *et al.* 2017; Weimerskirch *et al.* 2018), marine mammals (Sweeney *et al.* 2016; Ramos *et al.* 2018) and Red-winged Blackbirds (Wandrie *et al.* 2019). This pattern is possibly due to drones approaching on a direct path potentially resembling a potential predator that has discovered prey. There was also one study that noted Brown Skuas *Stercorarius antarcticus* approaching within 3 m of their drone during vertical ascent but losing interest after the

drone commenced horizontal sweeping (McClelland *et al.* 2016). These results were possibly influenced by other factors such as changes in noise emissions (Mustafa *et al.* 2017; Weston *et al.* 2020). In contrast, two studies reported stronger reactions to drones flown horizontally than vertical descents; in these studies, Ramos *et al.* (2018) used their drone to follow Common Bottlenose Dolphins *Tursiops truncatus* in locomotion, whereas Bennitt *et al.* (2019) used drones to approach mainly stationary African Bush Elephants *Loxodonta africana* and ungulates.

Two studies found that launching drones in a direction away from waterbirds and reaching survey altitude before approaching them elicited fewer negative reactions as opposed to launching the drone towards them (Jones *et al.* 2006; McEvoy *et al.* 2016). There was also one study that found that Red-winged Blackbirds were more susceptible to disturbance from drones performing direct approaches towards them compared to overhead flights (Egan 2018).

Four studies reported increase disturbances associated with drones positioned directly above affected animals. In two of these studies, the action of hovering directly above elicited stronger reactions than overhead sweeping flights in Australian Fur Seals (McIntosh *et al.* 2018) and Black-handed Spider Monkeys *Ateles geoffroyi* (Spaan *et al.* 2019). Two other studies noted drone flights over seabird colonies eliciting stronger reactions from individuals situated directly below the flight path compared to individuals further away (Rush *et al.* 2018; Mapes *et al.* 2020).

Three studies found that different angles of approach had no effect on their subject animals, however in two of these studies, other factors were causing animals to flush (Brisson-Curadeau *et al.* 2017; Barnas *et al.* 2018a). The third study related to Southern Right Whales *Eubalaena australis* that exhibited no observable reactions to drone flights (Christiansen *et al.* 2020).

Timing of drone flights

The potential influence of the timing of drone flights on animal responses was referenced in 47 publications, within which we recognised six specific attributes of timing (Table 1). Only two publications referenced the frequency of drone flights, however the potential effects of animals being exposed to consecutive flights (or multiple flights within the same day) were referenced by 23 publications. Ten of these provided accounts of how animals responded to drones across repeated flights. In six studies, subject animals exhibited some level of habituation during subsequent flights, observed as either reductions in the proportion of individuals in colonies exhibiting negative reactions during subsequent flights (Brisson-Curadeau *et al.* 2017; Rümmler *et al.* 2018; Mapes *et al.* 2020), or individual animals that approached or moved away from drones during initial flights losing interest afterwards (Ramos *et al.* 2018; Rush *et al.* 2018; Ditmer *et al.* 2020).

The taxa in these studies were seabirds, passerines, bears and cetaceans. Contrarily, four publications reported no apparent changes to the level of negative reactions to drones across consecutive flights, three studies relating to seabirds (Rümmler *et al.* 2016; Brisson-Curadeau *et al.* 2017; Mustafa *et al.* 2017) and one study relating to sirenians (Ramos *et al.* 2018). Further, two publications reported subsequent flights resulting in increased levels of vigilance in Black-handed Spider Monkeys (Spaan *et al.* 2019) and fleeing in Eastern Grey Kangaroos *Macropus giganteus* (Brunton *et al.* 2019).

Of the publications that referenced consecutive flights, seven also referenced the importance of allowing intervals between consecutive flights to allow animals to resettle from potential disturbances. Intervals between flights were either proposed as a destined amount of time (e.g. five min in Brisson-Curadeau *et al.* 2017) or a variable amount of time based on observers perceiving animals to have resettled (Rümmler *et al.* 2016, 2018).

The duration of individual flights was referenced in 21 publications. Two of these studies reported how subject animals responded to drones over the course of flights, both of which related to marine mammals. Giles *et al.* (2021) observed increased duration significantly increasing the probability of Common and Indo-Pacific Bottlenose Dolphins *Tursiops aduncus* exhibiting negative reactions to drones, whereas Ramos *et al.* (2018) also studied Common Bottlenose Dolphins and found his subjects only reacting during initial drone approaches. However, the latter study also reported Antillean Manatees *Trichechus manatus manatus* reacting negatively throughout the course of drone flights irrespective of duration (Ramos *et al.* 2018).

Similar numbers of publications referenced the potential influence of time of day (n=10) and time of year (n=9) on animal responses. Although these may be regarded as environmental factors, we classed them as controllable factors based on drone pilots being able to choose the daily and seasonal timing of their activities. Two publications provided observations of animal responses over different times of day; Fettermann *et al.* (2019) reported Common Bottlenose Dolphins performing side-floats, a behaviour associated with vigilance, being statistically more frequent during mornings than afternoons; whereas, Rexer-Huber and Parker (2020) recorded no differences in New Zealand Fur Seal *Arctocephalus forsteri* and seabird responses at different times of day. Three other publications reported research methods that minimise adverse impacts on animals by avoiding certain times of day. Two of these related to avoid interfering with nest changeovers in Glossy Ibis *Plegadis falcinellus* pairs (Afán *et al.* 2018), and another in which times of days when thermals were present were avoided to minimise flights coinciding with Wedge-tailed Eagles *Aquila audax* (a non-subject species that potentially attacks drones) being active (Lyons *et al.* 2018). A third publication suggested that studies using thermal cameras

to detect mammals could employ nocturnal flights to minimise disturbance by possibly reduce the probability of animals visually detecting drones (Kay *et al.* 2019); however, there may be other issues associated with nocturnal flights such as permitting or drone pilots avoiding collisions in substantially reduced visibility.

Only two publications provided observations of animal responses varying at different times of year, both relating to predatory birds and their breeding status. In both cases, aggression towards drones in flight occurred during the breeding seasons of Ospreys *Pandion haliaetus* (Junda *et al.* 2015), Australian Magpies *Gymnorhina tibicen* and Pied Currawongs *Strepera graculina* (Lyons *et al.* 2018) but not at other times. Junda *et al.* (2015) specifically noted that Ospreys became more aggressive as their breeding season progressed.

Pilot experience and competence

Pilot experience and competence were referenced in 34 publications (Table 1), however none examined how this factor specifically influences animal responses to drone flights. This controllable factor relates to the ability of pilots to adequately control drones in flights to be considerate of other controllable factors, as well as avoid collisions. We found references to pilot experience and competences where publications deliberated on pilot certifications and/or their level of training or reported professional drone pilots contracted to undertake their flights.

Habituation flights

Habituation flights involve drones being flown at a distance from animals but within their line of sight so they have some opportunity to be accustomed to the presence of drones prior to approach. The allowance of habituation flights was referenced in six publications, one review (Harris *et al.* 2019) and five research studies (Table 1); however, none of these publications specifically tested differences in animal responses with or without habituation flights. These research studies related to birds, specifically waterbirds and seabirds (Bierlich and Johnston 2016; Rümmler *et al.* 2016; Mapes *et al.* 2020) and Red-winged Blackbirds (Egan 2018; Wandrie *et al.* 2019).

Geographic location

The potential influence of geographic locations on animal responses was referenced in five publications, three reviews relating to seabirds and marine mammals (Smith *et al.* 2016; Borrelle and Fletcher 2017; Mustafa *et al.* 2018) and two research studies (Table 1). The first research study reported Harbour Seals from a frequently disturbed colony exhibiting few reactions to drone flights than conspecifics at a more isolated colony that were disturbed by drones at higher approach distances (Pomeroy *et al.* 2015). Contrarily, the second research study suggested that exposure to less human interference may explain some discrete populations

of dolphins exhibiting fewer reactions to drone flights (Giles *et al.* 2021). Similar to time of day and time of year, geographic location may be considered an environmental factor, however in this context, drone pilots are able to choose the locations they conduct their activities.

Environmental factors potentially influencing animal responses to drone flights

The most referenced environmental factor was taxa of subject animals (n=58), followed by biological state of animals (n=32) and ambient noise (n=22) (Table 2).

Taxa

Of the publications referencing different taxa exhibiting variability in responses to drone flights, only one publication specifically referenced the array of visual acuity between taxa (Mesquita *et al.* 2020). Corresponding with many publications referencing drone noise as a potential factor influencing animal responses, four publications referenced the array of auditory acuity between taxa (Scobie and Hugenholtz 2016; Erbe *et al.* 2017; Rees *et al.* 2018; Mapes *et al.* 2020).

Seventeen research studies reported observations showing variations in animal responses to drone flights between different taxa. The majority were variations in responses between species of birds (n=11), mostly seabirds and waterbirds. Other studies reported differences in responses between seabirds and pinnipeds sharing the same habitats (Adame *et al.* 2017; Rexer-Huber and Parker 2020), seabirds and marine reptiles (Bevan *et al.* 2018), different species of marine mammals (Pomeroy *et al.* 2015; Ramos *et al.* 2018) and different species of terrestrial mammals (Bennitt *et al.* 2019). Reported differences between taxa were mostly expressed in terms of variations in the thresholds of controllable factors at which animals elicited negative reactions (e.g. Weston *et al.* 2020). Others were reported in terms of the time taken for flushed animals to return to their original position, typically for colonial animals (e.g. Mapes *et al.* 2020).

Biological state of animals

The majority of publications referencing biological state specifically referenced breeding status (n=31) (Table 2). We found nine publications that reported observations of variations in responses to drone flights between breeding and non-breeding individuals of the same species, the majority of which related to seabirds (n=6). Consistent amongst these observations, birds brooding eggs or chicks were less likely to flush than non-breeding individuals, which is consistent with parent birds prioritising defence of offspring they have invested in (Thys 2019). Further, Rümmler *et al.* (2018) observed reduced sensitivity to drone flights in Adélie Penguins *Pygoscelis adeliae* later in the chick-rearing season, speculating that perhaps less vigilance is required from parent birds when chicks are more

independent. The remaining three publications reporting varying responses between breeding stages related to birds of prey (Junda *et al.* 2016), passerines (Lyons *et al.* 2018) and pinnipeds (Pomeroy *et al.* 2015). Notably, drone surveys of birds undertaken by Beranek *et al.* (2021) followed recommendations from Lyons *et al.* (2018) to refrain from drone flights during the breeding seasons of some species to avoid provoking attacks. Observations of Gray Seals *Halichoerus grypus* by Pomeroy *et al.* (2015) followed the pattern of many seabirds that breeding females were less likely to flee than non-breeding individuals.

The moulting status of animals was the second recognised attribute of biological state. Although five publications referenced this factor, three of them (Kidawa *et al.* 2016; Fiori *et al.* 2017; Johnston *et al.* 2017) were only citing evidence in Gray Seals provided by Pomeroy *et al.* (2015). In that study, moulting Gray Seals were found to be more easily disturbed by drones than non-moulting Gray Seals. A further publication speculated that Pink-footed Geese *Anser brachyrhynchus* being limited in flight capacity during stages of moulting (see also Portugal *et al.* 2018) may be more sensitive to aerial stimuli such as drones (Lee *et al.* 2019).

Ambient noise

Of the 22 publications that referenced ambient noise, only three publications described how ambient noise may influence animal responses to drone flights (Goebel *et al.* 2015; Arona *et al.* 2018; Pfeifer *et al.* 2019). All three were research studies on colonial animals and referred to the general principle of noise emissions from drones being masked by ambient noise if the latter is louder. Sources of ambient noise reported in these publications included vocalisations from colonial animals (Pfeifer *et al.* 2019) and weather variables such as sea state and wind (Goebel *et al.* 2015).

Presence of conspecifics

The potential influence of conspecifics being present on animal responses to drone flights was referenced in 21 publications (Table 2). Three publications considered solitary animals versus others of the same species occurring in a group. One research study found that African Bush Elephants fled from drones irrespective of being solitary or in herds (Hahn *et al.* 2017), whereas the other two publications suggest that animals being solitary or in groups has some effect. One review on marine mammals and birds postulated that solitary animals would be more sensitive to drone flights than the same species within a group (Mustafa *et al.* 2018). Contrarily, a research study on Guanacos found that individuals in herds (more than 17 Guanacos) were more likely to react to drones than lone individuals (Schroeder *et al.* 2020).

The majority of publications that referenced the presence of conspecifics specifically referenced the number of

animals within a group as a potential influence on their responses ($n=19$). Nine of these publications provided specific observations showing the effects of group size, covering seabirds, waterbirds, marsupials, ungulates, pinnipeds and cetaceans. A larger proportion of these were research studies that found larger groups being more easily disturbed by drone flights (Barr *et al.* 2020; Giles *et al.* 2021; Jarrett *et al.* 2020; Schroeder *et al.* 2020), which can be explained in part by other researchers observing negative reactions in individual seabirds, waterbirds and pinnipeds triggering others in their colonies to subsequently react (McIntosh *et al.* 2018; Mapes *et al.* 2020; Dundas *et al.* 2021). Only two publications reported animals exhibiting fewer negative reactions to drone flights when in larger groups. The taxa in these research studies were kangaroos (Brunton *et al.* 2019) and seabirds (Raout *et al.* 2020).

Weather variables

The potential influence of weather variables on animal responses to drone flights was referenced in 20 publications (Table 2), the majority of which referenced wind ($n=15$). Two publications reported specific evidence of wind influencing animal responses. First, as discussed earlier, Ditmer *et al.* (2015) recorded more elevated heart rates in American Black Bears during drone flights in windy conditions. Second, Rischette *et al.* (2020) found different effects of windspeed in their study of Sharp-tailed Grouse *Tympanuchus phasianellus*; windspeeds between 6-13 km per hour were optimal for minimising flushing during drone flights, possibly because lower windspeeds caused noise emissions from drones to be more easily perceived by grouse while higher windspeeds forced an increase in flight angle in order to maintain a linear flight path, causing their drone to emit more noise. In contrast, three other research studies found that windspeed had no statistically significant effect on responses to drones in Adélie and Gentoo Penguins *Pygoscelis papua* (Rümmler *et al.* 2016; Mustafa *et al.* 2017), Common Bottlenose Dolphins and Antillean Manatees (Ramos *et al.* 2018).

One research study also avoided drone flights in high winds due to Wedge-tailed Eagles being known to be more likely to be active in those conditions (Lyons *et al.* 2018). Numerous other studies also avoided conducting drone flights in high winds, however their rationale only considered the practical difficulties of controlling drones in these conditions; hence, these publications were not included in this part of our review.

Sea state was referenced in five publications, however only one provided evidence of its effects on animal responses during drone flights. This research study recorded chin-slaps in Common Bottlenose Dolphins occurring more frequently during drone flights conducted when sea state was 1 on the Beaufort scale than 2 (Fettermann *et al.* 2019). Fewer publications referenced cloud cover ($n=3$),

however all three of these publications provided evidence of its effects on animal responses. One research study found increased stress behaviours in dolphins in cloudy conditions compared to sunny conditions (Fettermann *et al.* 2019), with another study suggesting that cloud cover renders drones of any colour as dark objects, potentially resembling aerial predators (Mapes *et al.* 2020). However, another dolphin study contrarily found that increased cloud cover was associated with a significant decrease in stress behaviours (Giles *et al.* 2021).

Habitat variables

The potential influence of habitat variables on animal responses to drone flights was referenced in 19 publications (Table 2). Seven publications also referenced the potential effects of geophysical differences, for example, animals in water versus animals on land, or animals on seashores versus animals further inland. However, only one publication reported research results explicitly showing variations in the same species' responses to drone flights in different geophysical environments. This research study found that disturbance to waterbirds from drones was more likely to occur at coastal sites than agricultural land and inland lakes, and more likely to occur at agricultural land than inland lakes (Jarrett *et al.* 2020).

Six publications referenced the potential influence of vegetation type and density, however only one research study reported explicit evidence of study species being more likely to flee in open habitats than closed habitats (Bennitt *et al.* 2019). A further publication postulated that vegetation height may play a role in obscuring waterbirds' view of surroundings, causing them to be more sensitive to stimuli (Jarrett *et al.* 2020). In contrast, Allport (2016) observed Whimbrels being aware of a drone behind a wall of vegetation by its noise emissions and postulated that vegetation obstructing their view of the drone delayed flushing, which subsequently occurred when the drone was no longer behind this vegetation.

Three publications referenced the potential influence of water clarity, one of which reported evidence of the association between water clarity and animal responses to drone flights; Giles *et al.* (2021) found that increased water clarity was associated with a significant decrease in the probability of dolphins exhibiting negative reactions. In contrast, Bevan *et al.* (2018) postulated that reduced water clarity may reduce the likelihood of aquatic animals visually perceiving drones flown overhead.

Behavioural state of animals

The potential influence of the animals' behaviour on their subsequent responses to drone flights was referenced in 15 publications (Table 2). The majority of these publications were referencing the specific activity of animals at the time drones were launched ($n=13$), for instance a resting animal versus an animal actively

engaged in foraging or grooming. Inman *et al.* (2019) postulated that resting animals may not react as strongly to stimuli as animals engaged in active behaviour. Additionally, Bevan *et al.* (2018) surmised that the activities of animals prior to drone flights may influence the threshold at which approach distances elicit responses in animals. However, in their study, drones were flown over nesting sea turtles and no disruptions to any stages of nesting were observed. Similarly, Jarrett *et al.* (2020) found that the likelihood of waterbirds reacting negatively to their drones was not significantly affected by their activity prior to drone flights, though this finding was likely owing to subject animals' overarching sensitivity to drones at particular sites. Of the 13 publications referencing pre-flight activity of animals, only one research study provided evidence of animals responding differently to drone flights based on their current behaviour; Giles *et al.* (2021) recorded drone flights eliciting the most frequent negative reactions in dolphins when they were socialising as opposed to travelling, resting, milling or foraging.

Two publications also considered whether birds were present in the airspace that the drone would be flown in prior to launch (Raoult *et al.* 2020; Rexer-Huber and Parker 2020). This factor was a precaution considering the likelihood of disturbances caused by drones being flown in amongst flying animals, these animals potentially attacking drones and/or animal-aircraft collisions.

Exposure to anthropogenic settings

The level of human presence and other anthropogenic settings at certain locations were considered as potential factors influencing animal responses to drone flights in 19 publications (Table 2). Six publications suggested that certain animals exhibiting fewer negative reactions than conspecifics were possibly due to some level of habituation. None of these notions were systematically tested, except perhaps Wandrie *et al.* (2019) finding that captive and wild Red-winged Blackbirds differed in their responses to approach distances of 15 m, the latter exhibiting negative reactions. Other publications noted subject animals in more urbanised areas or locations frequently visited by humans exhibiting fewer or less intense reactions to drone flights; taxa in these research studies were pinnipeds (Pomeroy *et al.* 2015), kangaroos (Brunton *et al.* 2019), waterbirds (Jarrett *et al.* 2020). Further, Thompson (2018) noted some habituation in Greater Sage-grouse *Centrocercus urophasianus* after four days of researchers being present near a lek, and Inman *et al.* (2019) surmised that noise emissions from their drone may have had lessened effect on a Common Hippopotamus *Hippopotamus amphibius* pod due to the proximity of an airstrip to their lagoon. Contrarily, one publication noted a possible case of dolphins being less reactive to drone flights in areas that receive lower levels of human visitation (Giles *et al.* 2021) compared to more visited locations.

Presence of predators

The potential influence of nearby predators on subject animal responses to drone flights was referenced in 15 publications (Table 2). The majority of these publications considered the risk to progeny when/if parent birds were flushed from their nests, though one research study demonstrated more intense disturbance in waterfowl during drone flights when birds of prey were present compared to other times (McEvoy *et al.* 2016). Apart for one publication considering nest predators of birds of prey nests (Junda *et al.* 2015), all other publications that referenced the presence of predators were in relation to aquatic birds being susceptible (Harris *et al.* 2019; Lyons *et al.* 2019b; Valle and Scarton 2018; Jarrett *et al.* 2020), specifically waterfowl (McEvoy *et al.* 2016; Barnas *et al.* 2018a; Barnas 2019), waders (Valle and Scarton 2019, 2020), penguins (Rümmeler *et al.* 2016, 2018; Mustafa *et al.* 2017) and other seabirds (Brisson-Curadeau *et al.* 2017; Mapes *et al.* 2020).

Exposure to other anthropogenic disturbances during drone flights

The potential influence of other simultaneous anthropogenic disturbances on animal responses to drone flights was referenced in seven publications (Table 2). The taxa covered by these publications were penguins (Rümmeler *et al.* 2016, 2018), waterbirds (Barnas *et al.* 2018a), cetaceans (Torres *et al.* 2018; Horton *et al.* 2019; Giles *et al.* 2021) and marine animals collectively (Raoult *et al.* 2020). Sources of disturbances may include activities that drone pilots are responsible for (e.g. multiple people traversing the site or visual impacts or noise emissions of vehicles or marine vessels) or activities performed by other people (e.g. recreationalists or adjacent commercial activities).

Age of animals

The potential influence of the age of animals on their responses to drone flights was referenced in 11 publications (Table 2). Four publications investigated how different responses were between adult and younger age classes. Two of these publications reported adults exhibiting little to no negative reactions compared to younger age classes in King Penguins *Aptenodytes patagonicus* (Weimerskirch *et al.* 2018) and New Zealand Fur Seals (Rexer-Huber and Parker 2020). Contrarily, one research study reported adult Antillean Manatees being more susceptible to being disturbed by drone flights than younger age classes (Ramos *et al.* 2018). A further study found that adult Gray Seals and pups were both not visibly disturbed by drone flights (Arona *et al.* 2018), which is likely owing to some overarching tolerance of overhead drones at that particular colony.

Sex of animals

The potential influence of the sex of animals on their responses to drone flights was only referenced in four

publications (Table 2). Only one publication reported supporting observations in terms of breeding female Gray Seals being more resistant to fleeing than conspecifics (Pomeroy *et al.* 2015). This research study was subsequently cited by the three other publications (Kidawa *et al.* 2016; Fiori *et al.* 2017; Bevan *et al.* 2018).

Animal condition

The potential influence of the animals' physical condition on their responses to drone flights was only referenced in three publications (Table 2). These publications covered a diverse array of taxa but all referenced animal condition in general terms only. The reference was in relation to animals' biochemical state in two publications, one noting nutrition (Rümmeler *et al.* 2018) and the other noting hydration, hormone and stress levels (Bennitt *et al.* 2019). One further publication referenced animal condition in terms of whether animals were injured or sick (Gonzalez and Johnson 2017).

Discussion

The use of drones to approach wildlife is now a well-established practice and likely to continue growing in popularity and adoption (Barnas *et al.* 2020). Scientific literature on approaching wildlife with drones clearly demonstrates the variability in animal responses across different taxa, different ways drone flights are performed and the different circumstances they are deployed in. This growing body of information represent an invaluable resource for developing future policies that build on the standard operating procedures and best practice guidelines currently available (Gonzalez and Johnson 2017; Weston *et al.* 2020). The variability in animal responses between taxa highlights the need for taxa-specific protocols in some cases (Domínguez-Sánchez *et al.* 2018), especially for threatened species and/or animals sensitive to disturbance (Hodgson and Koh 2016; Ramos *et al.* 2018). Scientific literature also identified variability within species (Fettermann *et al.* 2019; Giles *et al.* 2021), which highlights the need for taxa-specific protocols to also account for geographical and biological variations. Variability within species may also occur from individual differences in animal behaviour (Moiron *et al.* 2020), which is yet to be explored in the context of animal responses to drone flights.

This review highlighted the broad number of factors that potentially influence the impact of drone flights on target and non-target wildlife. The number of publications referencing each factor is somewhat an indication of the pertinence of those factors. We found approach distance, noise emissions, airspeed, drone type and flight pattern to be the most prominent controllable factors in the scientific literature. Apart from taxa, breeding status of subject animals, ambient noise, weather and habitat variables and animals' levels of exposure to anthropogenic settings were the most prominent environmental factors

in the scientific literature. Factors also differed in their pertinence from many that were broadly applicable to a wide range of taxa and environments to some factors only applicable to certain contexts, such as water clarity to aquatic animals. Policies and protocols that address these factors have an increased probability of minimising or eliminating disturbance of drone flights in the future.

Several publications referenced controllable and environmental factors in terms of animals' ability to detect the presence of a drone. In general, reduced approach distances and noise emissions appear to increase the probability of animals perceiving the presence of drones. Faster airspeeds though have varying influences, increasing the probability of animals perceiving drones from a distance by emphasising the drone (Schroeder *et al.* 2020) or decreasing the probability of animals perceiving drones by reducing the length of time the drone is flown over individuals (Dundas *et al.* 2021). We also found numerous examples of linkages between factors, such as the effects of noise emissions reducing with increasing approach distance and also being masked by ambient noise (Arona *et al.* 2018). Additionally, ambient noise may be influenced by the size of a group of animals vocalising, windspeed and sea state (Goebel *et al.* 2015; Pfeifer *et al.* 2019). Such linkages highlight the need for drone pilots to evaluate controllable factors in context with other controllable and environmental factors. We recommend that managers, government officials and researchers take a holistic approach considering these interactions when developing policies and protocols.

Based on the general pattern that greater approach distances have a reduced likelihood of causing disturbance to wildlife, we recommend the selection of conservative approach distances, especially for animals known to exhibit stress responses to drone flights (Wang *et al.* 2019). We recognise that approach distances in research studies are generally selected to optimise the quality of results and that data collected at certain distances may lack the necessary accuracy and precision (Mulero-Pázmány *et al.* 2014; Brunton *et al.* 2020). Some publications reported thresholds of approach distance on animal responses being influenced by other controllable factors such as drone characteristics and environmental factors such as breeding status and conspecifics being present (Pomeroy *et al.* 2015; McIntosh *et al.* 2018). Therefore, for scenarios where a certain approach distance is necessary but likely to cause disturbance, researchers may be able to minimise disturbance by addressing other controllable factors.

Similar to approach distance, there was a consistent pattern that greater take-off distances reduced the probability of negative reactions in animals (Brisson-Curadeau *et al.* 2017; Rümmler *et al.* 2018). We therefore also recommend the selection of conservative take-off distances. As a secondary consideration, the location of launch is often where drone pilots are located during flights. Therefore, take-off distance as a

function of the distance between the pilot and subject animals also needs to be considered to reduce the overall risk of disturbing animals.

Our review found publications that encouraged not launching drones directly towards animals and avoiding direct approaches (Jones *et al.* 2006; McEvoy *et al.* 2016). These considerations were in relation to bird colonies but may be applicable to a broader range of taxonomic groups. However, we recognise that direct approaches may be unavoidable depending on the purpose of the drone flight, such as collecting samples from animals (Centelleghé *et al.* 2020). There were also observations of increased disturbance in animals directly below passing drones (Rush *et al.* 2018; Mapes *et al.* 2020) We therefore recommend that overhead flights avoid traversing directly above animals if/when possible.

Publications that referenced consecutive flights differed in observed animal responses during subsequent flights (Brisson-Curadeau *et al.* 2017; Mustafa *et al.* 2017). In cases where some level of habituation is observed (Mapes *et al.* 2020), it may be interpreted that undertaking multiple flights is unlikely to be impacting. However, in cases where the level of disturbance is relatively the same (Rümmler *et al.* 2016) or intensifies during subsequent flights (Brunton *et al.* 2019), it may be interpreted that undertaking multiple flights has accumulative impacts on the animals. Similarly, whether animals habituate to drone flights has implications on considerations of flight duration. For animals that quickly habituate, we would expect that increasing flight duration would have little impact. However, for animals that do not habituate, negative responses to drones would remain consistent or intensify as flights progress (Ramos *et al.* 2018; Giles *et al.* 2020), such that we would expect disturbance to be sustained over the duration of flights. In these situations, reducing flight duration as much as possible is recommended.

The selection of times of year and geographic locations to conduct drone flights may be pertinent factors to consider for some taxa. Publications that referenced time of year predominately related to the influence of the breeding status of animals would have on their responses (Junda *et al.* 2016; Lyons *et al.* 2018). Where possible, we recommend avoiding conducting drone flights over animals during their breeding season, both to avoid impacts on reproductive success and nest predation and the likelihood of animals attacking drones in defence of their young. However, we recognise that researchers and managers may prefer to conduct drone flights during breeding seasons to gather scientific data on reproduction or utilise times when animals congregate (Rush *et al.* 2018; Mapes *et al.* 2020). We also recognise that some taxa are continuously in one breeding stage or another (Welbergen 2011), such that this recommendation cannot be readily adopted for such taxa.

Survey needs may also limit researchers' and managers' ability to select alternative geographic locations to conduct drone flights. Similar to the consideration of consecutive flights, geographic locations may be relevant due to different colonies of animals receiving varying levels of exposure to anthropogenic activity. Pomeroy *et al.* (2015) suggested that variations between pinniped colonies may be a result of variations in the resistance of particular individuals to stimuli, gradual habituation within the group or particular colonies being more prone to anthropogenic disturbance than others. However, Giles *et al.* (2020) considered geographic differences in dolphin responses to drone flights to be instead related to 'cultural differences' between populations of cetaceans (Whitehead *et al.* 2004).

Several research studies found drone flights deploying different configurations of controllable factors having no visible effect on animal responses (Chabot *et al.* 2015; Linchant *et al.* 2015; Afán *et al.* 2018). These cases were potentially indicative of an overarching tolerance to drone flights amongst those individuals of animals or groups. Conversely, several other studies found the same level of negative reactions irrespective of configurations to drone flight practices. These cases may reflect an overarching sensitivity in subject animals to drone flights. The careful consideration of drone flight practices for these situations is particularly pertinent. Some publications also referenced the risks of nest predation for breeding animals flushed from their nests by drone flights (Junda *et al.* 2015; Barnas *et al.* 2018a), which highlights how inadvertent impacts from drone flights may extend beyond the temporary disturbance of individuals. These concerns are probably also relevant to non-nesting taxa, considering that anthropogenic disturbances may cause animals to be separated from or abandon their young (Livezey 1990).

Some factors were referenced in a number of publications but were very limited in published evidence of their effects on animal responses. These factors included variations between the size (McIntosh *et al.* 2018) and colour of drones (Mapes *et al.* 2020), sexes of subject animals (Pomeroy *et al.* 2015) and levels of nutrition (Rümmler *et al.* 2018), hydration, hormones and pre-existing stress (Bennitt *et al.* 2019) and whether animals were sick or injured (Gonzalez and Johnson 2017). We therefore recommend that future studies investigating animal responses to drone flights incorporate some examination

of these particular factors. Nevertheless, further research of any controllable and environmental factors would likely provide valuable information for managers and other researchers performing drone flights.

The majority of research studies investigating the effects of drone flights on wildlife were limited to behavioural indications of disturbance. We found few examples where researchers used physiological parameters, and these were limited to measurements of heart rates (Ditmer *et al.* 2015; Howard *et al.* 2018; Weimerskirch *et al.* 2018) and respiration rates (Domínguez-Sánchez *et al.* 2018; Christiansen *et al.* 2020). The testing of stress hormones (such as cortisol) has also been used to assess animal responses to stimuli in other contexts (Pfefferle *et al.* 2018; Dixon *et al.* 2021) but we found no studies using such techniques to investigate animal responses to drone flights. The few cases physiological parameters were considered were immensely valuable in discerning disturbance even when negative reactions were impossible to observe visually. These findings have important implications on how purely visual studies should be interpreted, especially those that reported no visually observable responses to drones flown overhead. We therefore recommend conservative interpretations of any studies limited to visual observations of animal responses.

Research studies are generally subject to thorough assessments for ethical considerations (Beauchamp and DeGrazia 2020), which potentially accounts for the numbers of studies we found that reported no visible effects of drone flights on animal responses. However, drones are commercially available as off-the-shelf products and are being used around wildlife for a broader spectrum of applications, including civilian purposes (Rebolo-Ifrán *et al.* 2019). This reinforces the need for policies and best practice guidelines to be developed to equip drone pilots seeking to minimise impacts from their activities on animal welfare and conservation.

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