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Review

Trends and current state of research on greater one-horned rhinoceros (*Rhinoceros unicornis*): A systematic review of the literature over a period of 33 years (1985–2018)

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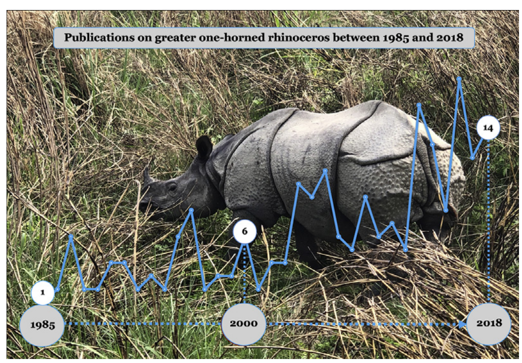
HIGHLIGHTS

- We reviewed 215 articles to identify the research gaps for rhinoceros conservation.
- The increasing population trends of rhinoceros is a great conservation success.
- Research on rhinoceros is skewed towards biological aspects of the species.
- Publications on genetics, diseases, habitat dynamics and impacts are limited.
- Evidence that implementation of conservation strategies helps conserve rhinoceros.

GRAPHICAL ABSTRACT



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ABSTRACT

Greater one-horned rhinoceros (*Rhinoceros unicornis*) is one of the most iconic wildlife species in the world. Once reduced to fewer than 500 during the 1960s, its global population has been recovering and is now over 3500, thanks to effective conservation programs in India and Nepal, the only two countries in the world where this species is found. It is one of the greatest success stories in biodiversity conservation given that hundreds of other species have disappeared, and thousands of species are on the verge of extinction. However, poaching is not the only threat for the long-term survival of rhinoceros. Loss and degradation of grassland habitat and the drying-up of wetlands are emerging threats predicted to worsen in the future, but the published information on rhinoceros has never been synthesized. In order to better understand the trends and current status of rhinoceros research and identify research gaps inhibiting its long-term conservation, we analyzed the themes discussed in 215 articles covering a period of 33 years between 1985 and 2018. Our findings suggest that studies on both free-ranging and captive rhinoceros are skewed towards biological aspects of the species including morphology, anatomy, physiology, and behaviour. There are no studies addressing the likely effects of climate change on the species, and limited information is available on rhinoceros genetics, diseases, habitat dynamics and the impacts of tourism and other infrastructure development in and around rhinoceros habitat. These issues will need addressing to maintain the conservation success of greater one-horned rhinoceros into the future.

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Contents

1. Introduction

Greater one-horned rhinoceros (*Rhinoceros unicornis*; "rhinoceros") once existed across the entire northern part of the Indian subcontinent along the Indus, Ganges and Brahmaputra River basins from Pakistan to the Indian-Myanmar border (Rookmaaker, 1983; Foose and van Strien, 1997; Talukdar et al., 2008; Rookmaaker et al., 2016). The population and geographical range sharply declined during the early 20th century due to loss of habitat (Gee, 1952; Talukdar et al., 2008; DNPWC, 2017) as a result of human activities (Poudyal et al., 2009; Puri and Joshi, 2018) and climatic changes (Choudhury, 1985; Li et al., 2015). The current distribution of rhinoceros is limited to a few protected areas in India and Nepal, totalling <20,000 km^2 (Talukdar et al., 2008; DNPWC, 2017).

By the early 20th century, there were only 200 rhinoceroses surviving in India and the species was on the brink of extinction (Ali, 1950; Rookmaaker et al., 2016). The population in today's Kaziranga National Park (KNP) was estimated to contain fewer than 20 individuals when hunting was banned in 1908 (Laurie, 1982). Due to successful conservation efforts, the rhinoceros population in KNP recovered to 1800 individuals by 2006 (Martin et al., 1987) and expanded into neighbouring areas including Pabitora and Orang Wildlife Sanctuaries (Talukdar et al., 2008). In Chitwan valley of Nepal, a population of >1000 individuals persisted until 1950 which then plummeted to 60–80 individuals by 1962 due to poaching and land clearing (Laurie, 1978; Dinerstein and McCracken, 1990; Dinerstein, 2003). As a result of effective anti-poaching measures, the population recovered to >600 animals in 2000 (Thapa et al., 2013). Its current global population in the wild is estimated to be approximately 3550 individuals (Rookmaaker et al., 2016; Talukdar, 2018).

Rhinoceros is an umbrella species (Amin et al., 2006) which, if adequately protected, also confers protection to a large number of naturally co-occurring species (Roberge and Angelstam, 2004). The rhinoceros is also a flagship species (Borthakur et al., 2016; Cédric et al., 2016; Rookmaaker et al., 2016) listed as 'vulnerable' on the IUCN Red List (Talukdar et al., 2008). The International Union for Conservation of Nature (IUCN) is responsible for developing and updating the Red List of Threatened Species, which is the world's most comprehensive inventory of the global conservation status of biological species (IUCN, 2019). Rhinoceros is protected by national legislation in both Nepal and India (Rookmaaker et al., 2016). It is a habitat specialist, and prefers the tall grasslands of floodplains and riverine forests (Laurie, 1978; Dinerstein, 2003). Rhinoceros also requires plenty of waterholes to wallow in, to keep its body cool in hot temperatures (Talukdar et al., 2008; DNPWC, 2017).

Studies have suggested that inadequacy of available habitat is one of the major challenges for continued rhinoceros conservation (Talukdar et al., 2008; Kafley et al., 2015). Chitwan National Park (CNP) in Nepal has experienced a severe decline in both the quantity and quality of rhinoceros habitat due to encroachment of woodland, invasion of alien plants into grasslands, and silting up of wetlands (CNP, 2013, 2016). It is estimated that (1) >15% of the prime rhinoceros habitat in CNP has been invaded by *Mikania micarantha* vine (Subedi, 2012; Murphy et al., 2013) and (2) total grassland areas in the park have declined by over 50%. Grasslands represented ~20% of CNP during the 1970s but represented only ~9.6% in 2016 (CNP, 2016). This has led to spatial redistribution of rhinoceros in CNP, where its population is decreasing in the eastern parts and gradually increasing in the western part of the park (Subedi et al., 2013). In India, tall grasslands in KNP have declined by 6% in the 20 years between 1990 and 2009, mainly due to invasive plants and expansion of forested areas into grassland (Medhi and Saha, 2014). Pabitora Wildlife Sanctuary, which is the second most important rhinoceros area in India, has experienced a 35% increase in woodland and 68% decline in alluvial grassland over a period of 27 years between 1977 and 2004 (Choudhury, 2005; Sarma et al., 2009). Overall, the decline in both quantity and quality of rhinoceros habitat has been observed in both countries within its range, and this is projected to continue in the future. If left unaddressed, such habitat decline will affect the survival of this species (Talukdar et al., 2008).

Climate change has also been identified as a threat to global biodiversity conservation over the last few decades (Howden et al., 2003; Heller and Zavaleta, 2009; Watson et al., 2012). Species assemblages and ecosystem dynamics have started responding to the recent global climate shift (Walther et al., 2002; Bellard et al., 2012; Allen et al., 2018). Thus, conservation in the era of climate change should not only focus on the problems of past and present but should also anticipate and prepare for the likely climate characteristics of the future (Glick et al., 2011). It is critical that we have adequate knowledge to sustain a viable rhinoceros population in relation to current threats of poaching and habitat degradation, in addition to the anticipated threats of climate change. The primary purpose of this review is to describe the trends and current status of research on rhinoceros and identify the research needed to ensure their long-term conservation.

2. Materials and methods

2.1. Literature search

We followed the systematic review process suggested by Pullin and Stewart (2006) for conservation and environmental management (Fig. 1). We searched for peer-reviewed articles published between 1985 and 2018 in five web-based databases – Web of Science, Scopus, Google Scholar, JSTOR and Science Direct mainly for two reasons: (1) availability of database in Web of Science only after 1985; and (2) our particular interest in recent trends for finding the research gaps. We used the terms "Indian Rhinoceros" OR "Greater One-horned Rhinoceros" OR "*Rhinoceros unicornis*" in our searches. In total, we found 230 articles in Web of Science, 196 in Scopus, and 831 in Google Scholar (Fig. 1). Searches in JSTOR and Science Direct did not yield any relevant studies that were not already found in Web of Science, Scopus and Google Scholar (see below), and were therefore not considered further.

2.2. Selection criteria

We examined the title, abstract, and keywords of each paper and excluded all articles that were not related to greater one-horned rhinoceros. We retained articles on both free-ranging and captive populations. After removing duplicates, we found 108 relevant articles across all three databases, 42 articles in two of these three databases; 63 articles were found only in Google Scholar and two articles were found only in Scopus. We then extracted and reviewed information from the final 215 articles (Table S1).

2.3. Data compilation and analysis

We categorised each article based on: (1) whether it was related to wild or captive rhinoceros; (2) the type of research, i.e. empirical studies involving primary data sources or theoretical studies using secondary sources of information or other literature; and (3) thematic focus (Table 1), so that the changing focus and priorities of the research on rhinoceros could be evaluated. Complete details of each article are described in Table S1.

If an article contained information that related to more than one theme but discussed each theme equally, we counted the article under multiple primary themes. On the other hand, if an article focused on one major theme but also covered other themes to some extent, these other themes were counted as secondary themes. Because any one article could be recorded under one or more primary or secondary themes, sample sizes varied during our thematic analysis.

Data on rhinoceros population trends were extracted from available estimates given in relevant publications. In these studies, the population of free-ranging rhinoceros were estimated using the total block count method in protected areas known to contain rhinoceros (see below in Sections 3.5 and 4.4). The population data were primarily collected from publications by the Government institutions responsible for the management of rhinoceros in India and Nepal, as well as from the reports of the Asian Rhino Specialist Group. Information on the population of captive rhinoceros was obtained from international studbook records available online, which were analyzed to generate the distribution map of the captive rhinoceros in zoological institutions around the globe.

3. Results and discussion

3.1. Research trends on rhinoceros

Following publication of only one paper in 1985 (Fig. 2), the number of research papers on rhinoceros showed a gradual increase, with 30% (n = 65) of papers being published between 2014 and 2018.

We also detected a probable contribution of research to policy formulation. For instance, there were two papers published in 1995 in Nepal related to human-wildlife conflict, predominantly on human-rhinoceros conflict (Table S1). In 1996, the Government of Nepal promulgated the buffer zone management rules with a provision to declare buffer zones around national parks (Budhathoki, 2004). In fact, the general concept of buffer zone management emerged during the 1990s to mitigate the increasing human-wildlife conflict around protected areas in Nepal (Heinen and Mehta, 2000). Moreover, there is also

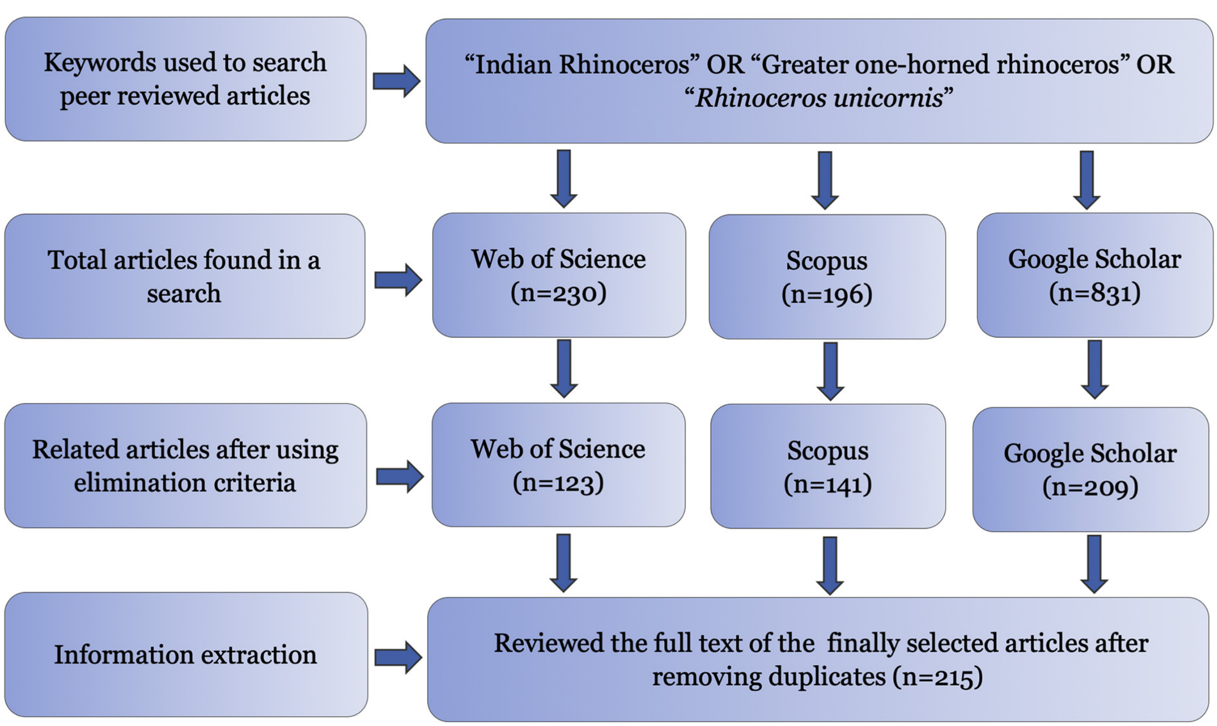

Fig. 1. Procedure of literature searching for our systematic review of the publications on greater one-horned rhinoceros globally.

Table 1
Thematic areas of the studies on greater one-horned rhinoceros and summary of key contents included in each thematic area.

SN	Thematic area	Key contents
1	Biology	Biological aspects of rhinoceros including morphology, anatomy, physiology, general behaviour, reproductive behaviour, and feeding behaviour.
2	Habitat	Distribution and space use patterns, habitat dynamics and habitat suitability analysis.
3	Genetics	Genetic variability, DNA barcoding, use of genetic techniques for population estimation.
4	Impact on species	Impact of tourism activities and other socio-economic developments on rhinoceros and its habitat.
5	Population	Demography, census and population trend and its management.
6	Capture and handling	Chemical immobilization, restraints, handling and translocation.
7	Poaching	Poaching of rhinoceros, anti-poaching strategies and activities.
8	Conflict	Human-rhinoceros conflict including crop depredation, human injuries and death, and activities to minimize conflict.
9	Disease	Diseases, its causes and treatment, parasites and pathogens.
10	Climate change	Likely impacts of climate change on rhinoceros and its habitat.

evidence that another problem related to rhinoceros poaching in India has directed research towards causes of poaching and possible ways for overcoming it. There were four papers published on poaching of rhinoceros in India between 1994 and 1996 (Table S1). This was the era when rhinoceros were extirpated from Manas National Park as poaching surged due to the political unrest in Assam, India between 1990 and 1995 (Martin, 1996; Sinha, 2011).

Publications on rhinoceros genetics began during the 1990s; six articles were published in this decade on various aspects of rhinoceros genetics, including genetic variation (Dinerstein and McCracken, 1990), classification of species based on molecular systematics (Morales and Melnick, 1994), inbreeding in captive rhinoceros (Baur and Studer, 1995), and DNA sequencing of rhinoceros (Xu et al., 1996; Xu and Arnason, 1997; Ali et al., 1999). Publications on rhinoceros habitat significantly increased from 2010 onwards (Table S1). Most of this research focused on habitat dynamics, such as change in grasslands and wetlands (Sarma et al., 2011; Medhi and Saha, 2014; Puri and Joshi, 2018), invasive species in grassland habitat (Lahkar et al., 2011; Murphy et al., 2013; Choudhury et al., 2016), and evaluation of rhinoceros habitat suitability (Sarma et al., 2011; Ojah et al., 2015; Rimal et al., 2018). This research focus may be attributed to the recent changes in rhinoceros habitat in both countries, described earlier.

We found that the 215 articles we reviewed were cited 3676 times until November 2019. The mean number of citations per article was 17 (range 0–156). Of all the themes studied, the highest average citations per article (n = 24) was for the climate change theme and the lowest (n = 9) was for the poaching theme. There were six articles with >100 citations, while 25 articles had no citations at all, and >50% (n = 13) of them were published between 2014 and 2018 (Table S1). Articles with >100 citations were published between 1988 and 2009, with most of them focussing on genetics (n = 4) and one each in biology and conflict. Further details are given in Table S1.

3.2. Spatial distribution of the research on rhinoceros

Out of 215 articles, 112 articles were solely related to free-ranging rhinoceros, 94 articles were about captive rhinoceros, five articles included both captive and wild rhinoceros, and four articles were related to fossil record analysis from its historical range. Of the research studies on free-ranging rhinoceros, most of the publications (n = 63) were from India, 46 articles were from Nepal and eight articles were from both countries (Table S1). Of all the protected areas (Table S2), the highest number of studies on rhinoceros were from CNP (n = 29, 19%) followed by KNP (n = 21, 14%) and Pabitora Wildlife Sanctuary (n = 17, 11%). Shuklapanta National Park has the lowest number of studies (n = 3, 2%). There were few studies (n = 3, 2%) on rhinoceros from outside protected areas in both countries.

KNP in India has the largest population (n = 2401, 68%) of rhinoceros (Rookmaaker et al., 2016; Talukdar, 2018) and CNP in Nepal supports the second-largest population (n = 605, 17%) (DNPWC, 2017).

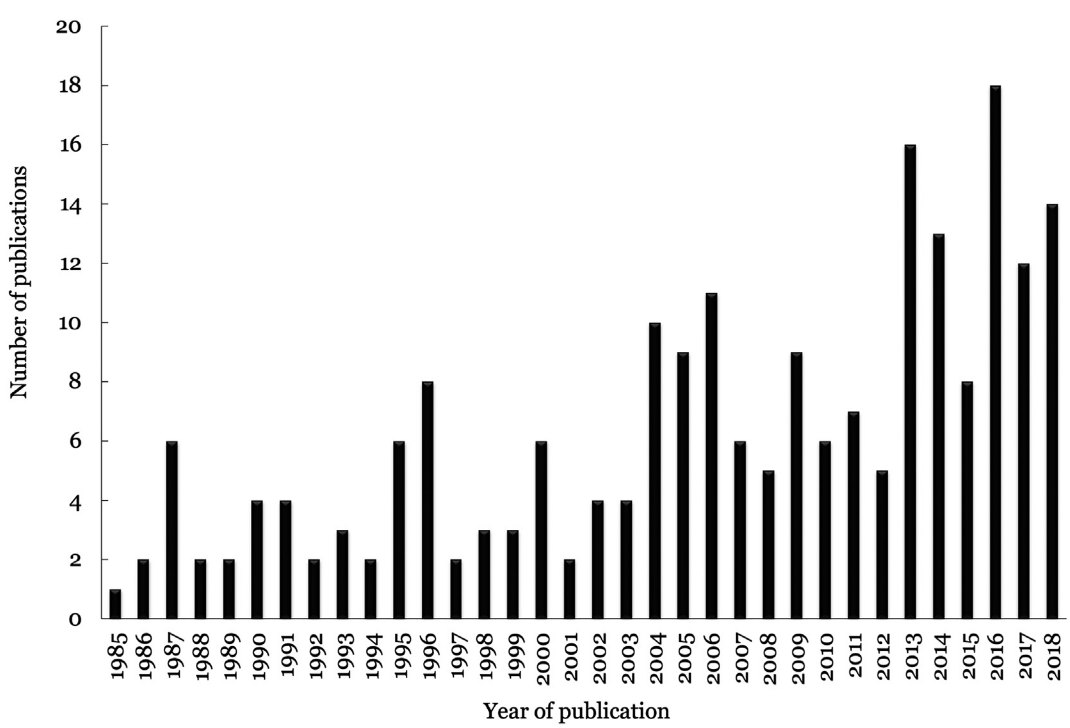

Fig. 2. The annual number of total publications on greater one-horned rhinoceros between 1985 and 2018.

However, 19% of the articles in this review were from CNP, and only 14% of the publications were from KNP. One of the reasons for this could be the involvement of international researchers on rhinoceros research in CNP, particularly during the 1980s (Table S1). Of the research papers on rhinoceros from Nepal, >50% were authored by international researchers (e.g. Dinerstein et al). The role of the National Trust for Nature Conservation (NTNC, formerly known as the King Mahendra Trust for Nature Conservation) – a non-governmental organisation established in 1982 for promoting research related to nature conservation – has been paramount in engaging foreign researchers through its global network, especially during the 1980s (NTNC, 2017).

In general terms, the available studies have covered the current rhinoceros-bearing protected areas in both India and Nepal. However, there is limited information on the movement of rhinoceros outside protected areas, and potential habitat for rhinoceros outside of these reserves. There is evidence of rhinoceros straying outside protected areas in both countries (Choudhury, 1996; Talukdar et al., 2007; Acharya and Ram, 2017; Rimal et al., 2018), but the population of rhinoceros outside the protected areas has declined sharply due to poaching and conflict with communities (Choudhury, 1996). Indian Rhino Vision 2020 aimed to increase the population of rhinoceros in Assam to 3000 by 2020 and spread them over seven protected areas: Kaziranga, Orang and Manas National Parks, as well as Pabitora, Laokhowa, Burachapori and Dibru Saikhowa Wildlife Sanctuaries (Puri and Joshi, 2018). Likewise, the rhinoceros conservation action plan of Nepal has proposed a feasibility study for rhinoceros habitat suitability in Koshi Tappu Wildlife Reserve (DNPWC, 2017). In recent years, 3–5 rhinoceros from CNP naturally migrated to adjoining Parsa National Park (PNP) and also wandered outside the protected areas to Rautahat and Sarlahi districts (Acharya and Ram, 2017; Rimal et al., 2018). Despite such records, there is minimal research on potential for rhinoceros conservation outside protected areas and its possible contribution to rhinoceros recovery and conservation.

There are 78 zoological institutions in 24 countries of the world (Fig. 3a) that keep greater one-horned rhinoceros (von Houwald, 2018). The studies on captive rhinoceros were carried out mainly in the United States (n = 30) and India (n = 22) followed by Germany (n = 6), the United Kingdom (n = 5) and Switzerland (n = 5), while only two articles originated from Nepal (Fig. 3b). The highest number of publications on captive rhinoceros (n = 77) were from countries outside their current in situ distribution.

3.3. Thematic focus of rhinoceros research

The thematic focus of rhinoceros research is summarized in Table 1 (see also Table S1). Publications on rhinoceros are predominantly concentrated on its biology for both the captive and wild populations (Fig. 4). The highest number of publications (n = 97) was on this theme, and the majority of them (n = 71) were from captive populations. Of the publications on free-ranging rhinoceros, the highest number was again related to biology (n = 28, 22%) followed by poaching (n = 22, 19%), population (n = 23, 18%) and habitat (n = 22, 17%). Three publications were related to the impact of tourism and other developmental activities on rhinoceros, whereas only one study was related to the impact of climatic change on rhinoceros. The study by Li et al. (2015) illustrates that synergistic effects of climatic change and intensified human impact has contracted the rhinoceros distribution range in the past, but there was no research that has directly studied the likely impacts of future climate scenarios on rhinoceros. In captivity, the highest number of publications was related to biology (n = 71, 69%), the second-highest (n = 14, 14%) was related to genetics, followed by disease and capture and handling (n = 4, 4%).

The biology thematic area has covered a wide range of topics including anatomy (Bhattacharya et al., 1987; Maluf, 1987; Bordoloi et al., 1993), morphology (Endo et al., 1996; Endo et al., 2009; Heidegger et al., 2016; Roth et al., 2018), general behaviour (Dinerstein et al., 1988; Hutchins and Kreger, 2006; Dutta and Mahanta, 2018), feeding behaviour (Dinerstein and Wemmer, 1988; Dinerstein, 1989, 1991b; Steinheim et al., 2005; Wegge et al., 2006; Pradhan et al., 2008; Hazarika and Saikia, 2012; Thakur et al., 2014; Deka and Sarma, 2015; Dutta et al., 2016), and reproductive physiology and behaviour (Dinerstein, 1991a; Schaffer et al., 1998; Yadav, 2000; Roth, 2006; Wojtusik et al., 2018). Likewise, the habitat thematic area includes studies related to invasive species on grassland habitat (Lahkar et al., 2011; Murphy et al., 2013; Choudhury et al., 2016), habitat change (Kushwaha et al., 2000; Rawat, 2005; Sarma et al., 2009; Medhi and Saha, 2014), current habitat suitability (Kushwaha et al., 2000; Sarma et al., 2011; Thapa et al., 2014; Ojah et al., 2015; Rimal et al., 2018) and one paper on future habitat suitability in its historical distribution range (Jiang et al., 2016).

In the thematic area of genetics, studies have covered broad issues including artificial insemination of captive rhinoceros for enhancing genetic diversity (Stoops et al., 2016), genetic structure and variability (Dinerstein and McCracken, 1990; Zschokke et al., 2011; Das et al., 2015; Zschokke, 2016), inbreeding and outbreeding in captive rhinoceros (Baur and Studer, 1995; Zschokke and Baur, 2002), genetic census of free-ranging rhinoceros for population estimation (Borthakur et al., 2016), and DNA barcode sequencing (Xu et al., 1996; Xu and Arnason, 1997; Ali et al., 1999; Kapur et al., 2003; Ghosh et al., 2013). Genetics has emerged as one of the priority areas of rhinoceros research in recent years. Under the thematic area of impact, there were only three publications that primarily studied the impacts of tourism and other developmental activities on rhinoceros (Choudhury, 1987; Lott and McCoy, 1995) and human impact on rhinoceros (Li et al., 2015). However, there are other publications that discuss threats to rhinoceros from human activities as a secondary theme (Choudhury, 2005; Sarma et al., 2009; Rimal et al., 2018).

A substantial number of articles have included more than one theme in their research (Table S1). Common secondary themes were again biology (n = 20), followed by poaching (n = 8), habitat (n = 5) and population size (n = 5). While 20% of the articles have studied more than one thematic area, the biology theme remains the primary focus for rhinoceros studies over the last three decades; conflict was the second major theme during the 1990s. Subsequent to this, poaching has reemerged as a priority research area given poaching escalated in this period in both India and Nepal due to political instability (Talukdar, 2000; Thapa et al., 2013). A sizeable number of publications have focussed on population status and management as well as habitat dynamics in recent years (Fig. 4, Table S1).

The rhinoceros is one of the most studied wildlife species in Nepal (DNPWC, 2017). However, the demography and ecology of this species is still relatively poorly known, compared to its African cousins (Cédric et al., 2016). The rhinoceros is a charismatic species, which has received national and international attention in terms of scientific study and is relatively well-studied in the wild as well as in captivity (Subedi, 2012). However, we still have inadequate information about the basic biology of the species, including density-dependent effects and how this mega-herbivore affects habitat quality and habitat availability when population density increases (Cédric et al., 2016).

3.4. Types and duration of rhinoceros research

We found that most publications on captive rhinoceros were based on primary sources of information or empirical studies (n = 90, 91%) and predominantly from the studies of <6 months duration (n = 84, 85%) (Fig. 5b). A nearly equal number of publications were based on primary (n = 61) and secondary sources (n = 56) of information for free-ranging rhinoceros (Fig. 5a). There were few papers published from research conducted over three years (n = 5) given that the majority (n = 77, 66%) were from research conducted under six months.

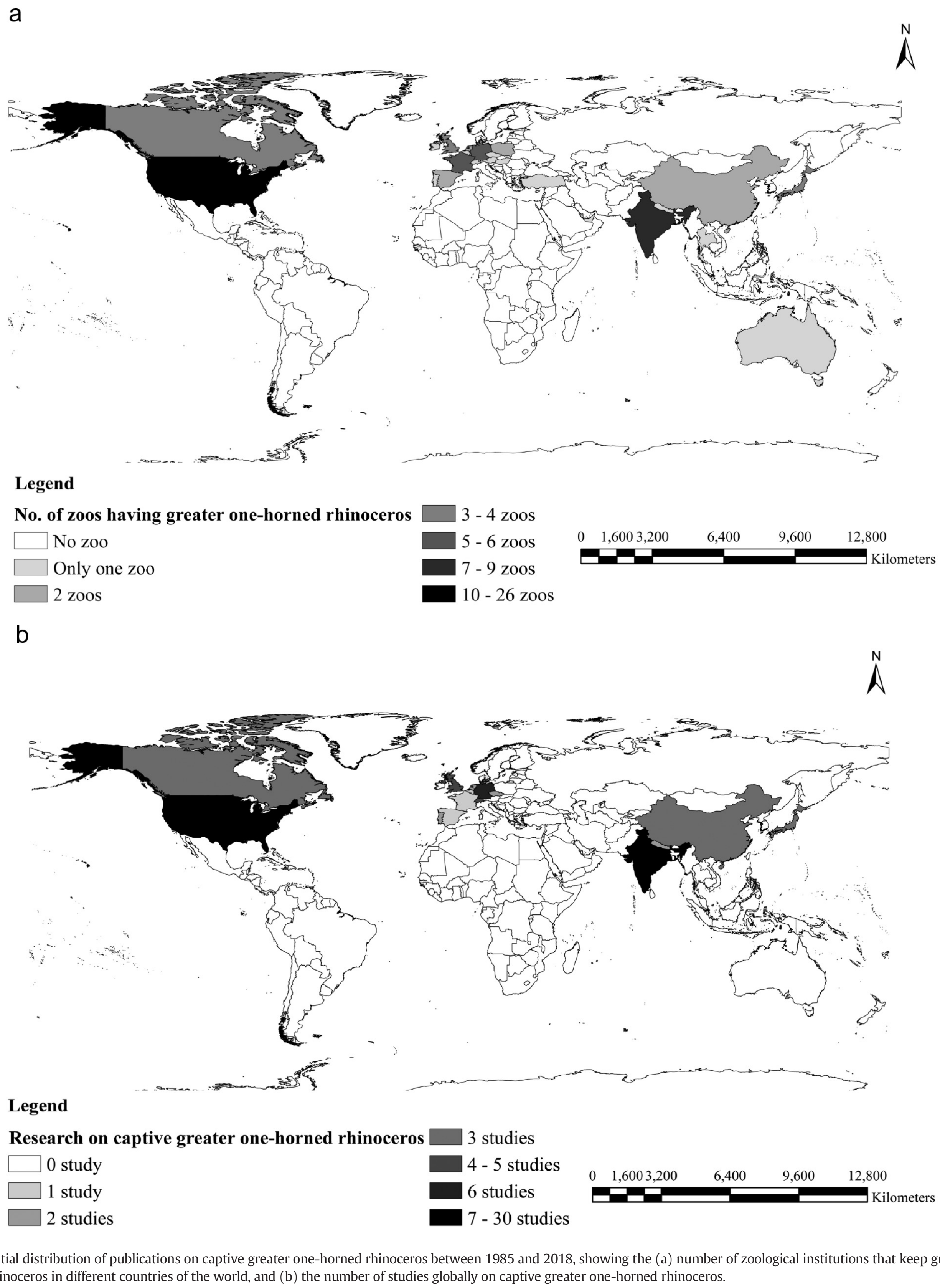

Fig. 3. Spatial distribution of publications on captive greater one-horned rhinoceros between 1985 and 2018, showing the (a) number of zoological institutions that keep greater one-horned rhinoceros in different countries of the world, and (b) the number of studies globally on captive greater one-horned rhinoceros.

Our analysis of the published literature on rhinoceros revealed limited empirical research conducted over longer timeframes. This is concerning given that managing the species in the context of climate change requires information on long-term monitoring of the species and its interaction with habitat components.

3.5. Population trends of rhinoceros

Population sizes of both free-ranging and captive rhinoceros have been gradually increasing since 1985 (Fig. 6; Table S2). The population of free-ranging rhinoceros in India was estimated to be nearly 1300 in

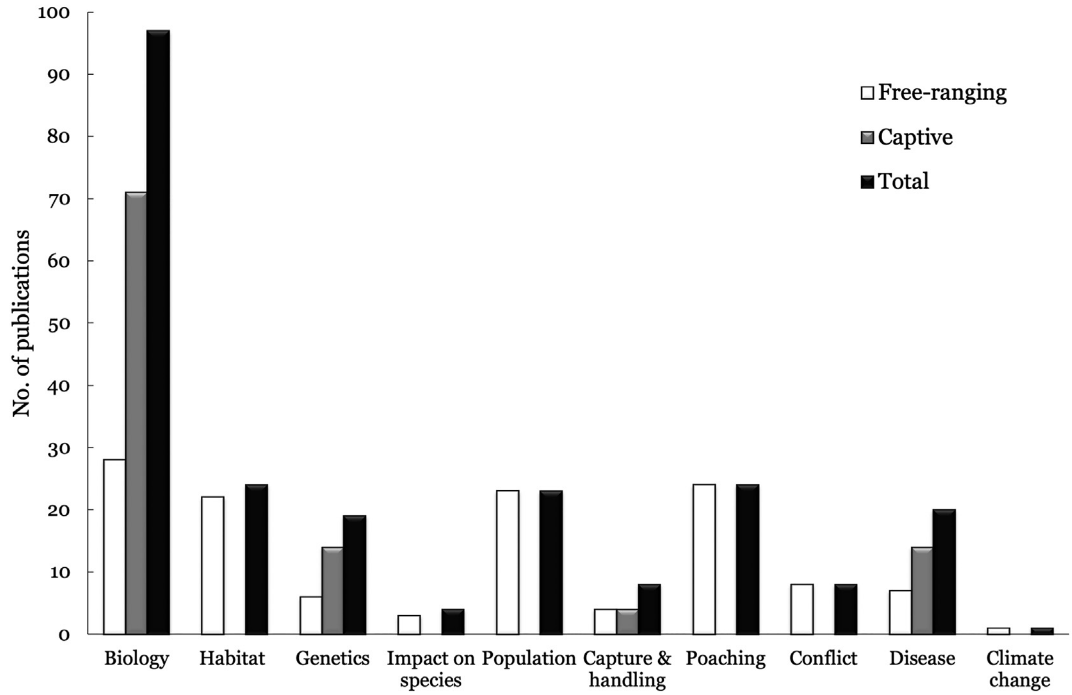

Fig. 4. Publications on greater one-horned rhinoceros in 10 different thematic areas.

1985 (Martin et al., 1987; Martin and Vigne, 2012), which had increased to >2900 individuals by 2015 (Rookmaaker et al., 2016; Talukdar, 2018). In Nepal, the rhinoceros population recovered well until 2000 (Thapa et al., 2013), however, it had decreased to 400 animals by 2005 due to escalated poaching owing to the civil unrest in the country (Poudyal et al., 2009). In recent years, the rhinoceros population has been gradually increasing and there are nearly 650 rhinoceros in Nepal today (DNPWC, 2017; Talukdar, 2018).

Periodic outbreaks of social unrest in parts of its range have resulted in specific population of rhinoceros being eliminated or substantially reduced (Amin et al., 2006). For example, rhinoceros disappeared from Manas National Park in Assam, India due to poaching that occurred during social unrest around the national park during the early 1990s (Talukdar, 2000). The Babai Valley of Bardia National Park in Nepal also experienced local extinction of rhinoceros during 2007 for similar reasons (Thapa et al., 2013). However, the population of free-ranging rhinoceros has still been increasing since the late 1960s (Amin et al., 2006; Martin and Vigne, 2012; Thapa et al., 2013; Rookmaaker et al., 2016; DNPWC, 2017; Talukdar, 2018). The current distribution of rhinoceros population in India and Nepal is presented in Fig. 7a and rhinoceros population trends between 1985 and 2015 in protected areas of India and Nepal are given in Table S2.

There were a total of 88 greater one-horned rhinoceros in captivity in 1985 (Molur et al., 1995). By 2000, its population in captivity increased to 137 animals (72 male and 65 female) in 50 zoological institutions. Of these 137 rhinoceros, 39 animals came from the wild, and 98 individuals were captive-born (Wirz-Hlavacek, 2001). There are 215 captive rhinoceros (111 male and 104 female) currently surviving in zoological institutions (Fig. 7b) around the globe (von Houwald, 2018). The United States of America has the highest number of zoological institutions that hold rhinoceros (n = 26), followed by India (n = 9) (von Houwald, 2018). Of all the captive-reared rhinoceros, only five animals (four males and one female) have ever been released back into the wild (von Houwald, 2016).

The overall conservation scenario of rhinoceros in both India and Nepal is encouraging given their increasing population trends (Table S2). This rhinoceros recovery is one of the great conservation success stories in the world, demonstrating that wildlife population can recover when provided with sufficient habitat and protection from key threats (Dinerstein and Price, 1991; Acharya, 2016; Aryal et al., 2017; Talukdar, 2018).

4. Implications for rhinoceros conservation

An analysis of the published literature from the last three decades has provided insights on various aspects of rhinoceros and its habitat. It also has revealed the pertinent issues and research gaps regarding the conservation of the species in the context of both ongoing and emerging challenges. Among other issues, the likely impacts of climate change on rhinoceros and its habitat, poaching, genetic implications and population dynamics need attention in order to ensure its continued recovery.

4.1. Climate change emerges as a threat to rhinoceros

Analysis of the literature revealed that there are no specific studies conducted on likely impacts of climate change on rhinoceros and its habitat. However, the rhinoceros conservation action plan for Nepal (2017–2021) has acknowledged that climate change is emerging as a serious threat to rhinoceros and that there is a knowledge gap concerning the impact of climate change on this and other wildlife species (DNPWC, 2017). The documented changes to hydrological cycles show that the warming climate increases the frequency and intensity of droughts (Huntington, 2006). Some recent climate-induced phenomena such as flash floods, prolonged droughts and frequent forest fires could have an effect on rhinoceros and its habitat. Extreme flooding is one of the most damaging natural hazards, and this is aggravated because of climate change (Ghosh et al., 2016). The analysis of data from 29 large river basins from around the world showed that the frequency of massive floods had increased substantially, and this trend will continue (Milly et al., 2002). In 1998, 39 rhinoceros drowned in KNP due to extreme flooding (Choudhury, 1998). In August 2016, 70% of KNP was flooded, including most of the grasslands favoured by rhinoceros (Ghosh et al., 2016). It is estimated that at least 141 rhinoceros have been killed by severe floods in KNP in total, and 12 rhinoceros were found dead in the flood episode of July 2019 alone (Sharma, 2019).

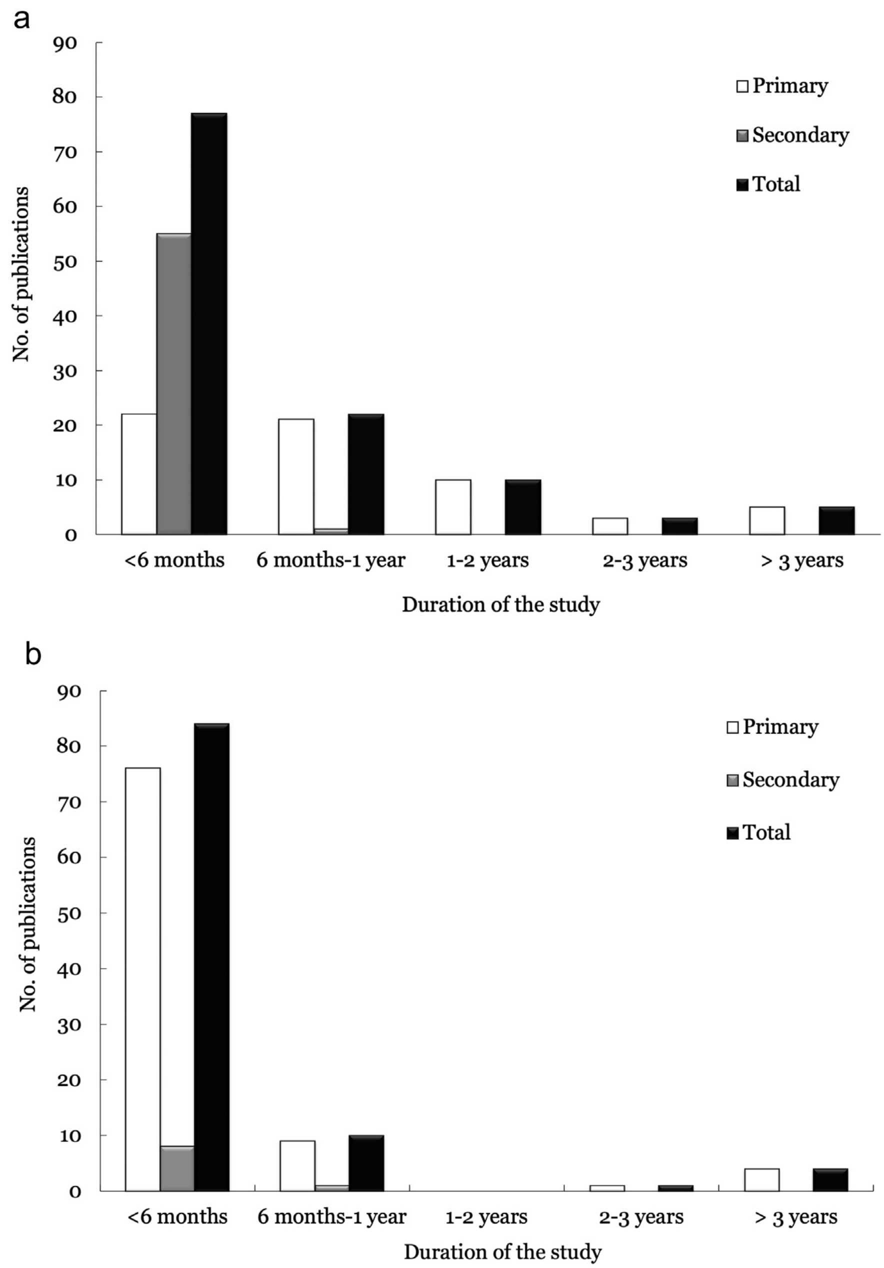

Fig. 5. Publications on free-ranging (a) and captive (b) greater one-horned rhinoceros based on types and duration of research.

The ecological changes associated with climate change exacerbate the existing pressures on natural systems (Glick et al., 2011). The abundance of rhinoceros has been increasing in Nepal, as poaching has been halted, primarily through successful implementation of anti-poaching programs (Acharya, 2016; Aryal et al., 2017). However, the recent trend in episodic natural deaths of rhinoceros is increasing; 95 rhinoceros have been found dead in CNP in the last three years due to unexplained 'natural' causes (Mandal, 2019). The reason behind the recent increase in natural deaths of rhinoceros is unknown.

The rhinoceros is a specialist in terms of habitat requirements such as grasslands and wetlands. The area of grasslands in CNP has sharply declined as compared to the area covered by grasslands during the 1970s (CNP, 2016). Likewise, woodland has increased and alluvial grassland has decreased in Pabitora Wildlife Sanctuary (Rookmaaker et al., 2016). This could be attributed to the increasing concentration of carbon dioxide in the atmosphere, which favours the growth of shrubs and trees, known as woody thickening (Eamus and Palmer, 2008). Climate change is likely to favour the spread of invasive species (Hellmann et al., 2008; Thuiller et al., 2008; Vitousek et al., 2017). Invasive plant species are increasingly invading the grasslands on which rhinoceros depend (Rookmaaker et al., 2016). Rhinoceros and other large herbivore populations have declined in areas with high *Mikania micarantha* infestation. Mikania is a major concern as it has the potential to destroy prime habitats of several threatened and important species (Murphy et al., 2013). A substantial portion of the prime rhinoceros habitat in CNP has already been invaded by mikania vine (Subedi, 2012; Murphy et al., 2013). The increasing invasion of weeds in Nepal and India's grassland habitats in the past decade needs immediate management intervention to ensure the long-term conservation of rhinoceros habitat (Lahkar et al., 2011).

The shift in spatial and temporal patterns in the availability of suitable habitat is one of the likely impacts of climate change (Parmesan, 2006; Thuiller et al., 2011). At this point, the rhinoceros population in CNP is gradually shifting towards western parts of the park (Subedi et al., 2013), which may be attributable to the shift in suitable habitat as a result of climate change. However, it needs long-term monitoring

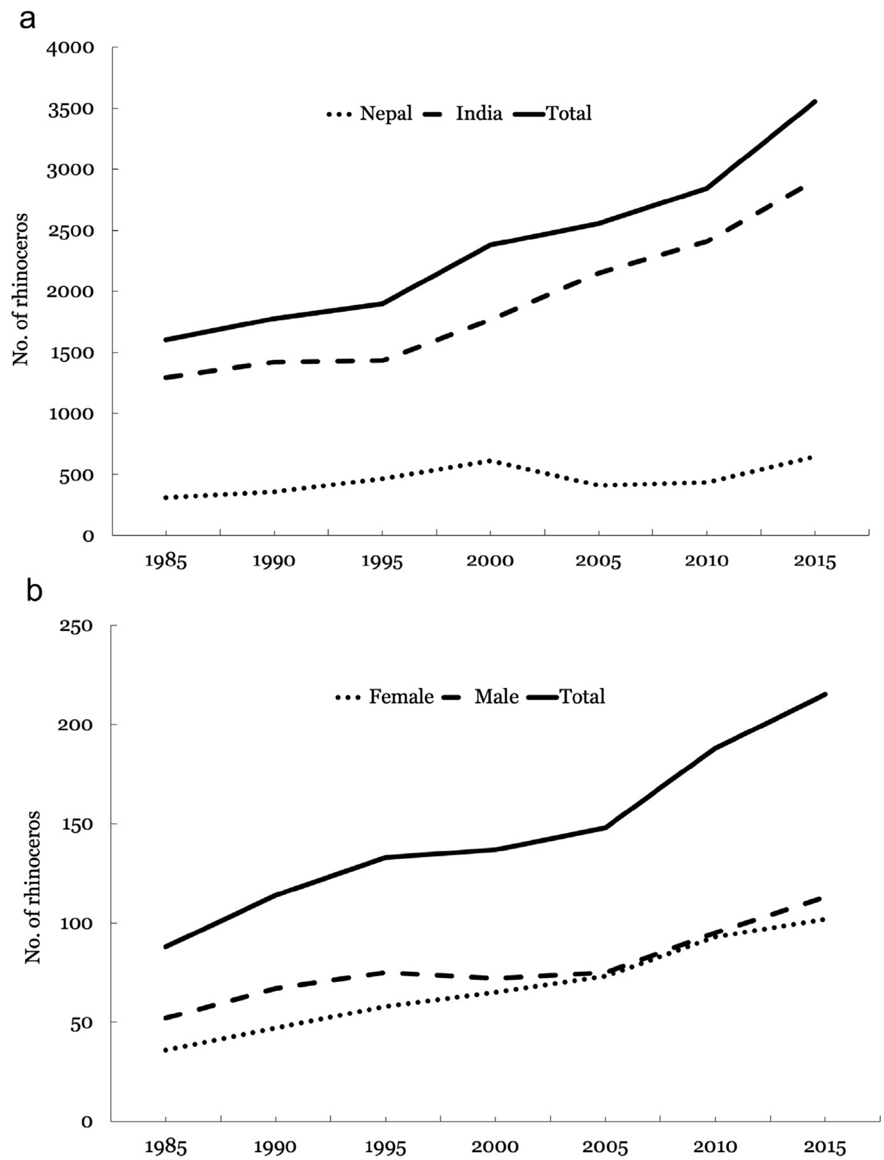

Fig. 6. Global population trends of greater one-horned rhinoceros between 1985 and 2015, showing (a) trends in free-ranging populations in both India and Nepal and (b) trends in captive populations (males and females) across all zoological institutions.

of the habitat dynamics to explore the causes of these changes. Based on the effects discussed above, climate change is likely to have impacts on rhinoceros and its habitat. As a result, climate change should be considered among the threats to rhinoceros, and its impacts should be mitigated as much as possible to ensure the long-term survival of the species.

4.2. Poaching remains a serious threat to rhinoceros

Rhinoceros losses to poaching between 1986 and 1995 was an estimated 450 in India and 50 in Nepal (Foose and van Strien, 1997), and during the 1990s, rhinoceros population was exterminated from Manas National Park in Assam, India due to social unrest around the park. Similarly, rhinoceros poaching increased in Nepal between 2001 and 2005 due to civil unrest in that country, which provided an opportunity for organised poachers to kill rhinoceros more easily (Talukdar, 2006). During this five-year period, at least 108 rhinoceros were poached in Nepal (Martin and Martin, 2006). National parks in Nepal are kept secure by the permanent presence of the Nepalese military in these areas. But most of the military security posts in CNP and BNP were temporarily abandoned due to Maoist rebel activity, enabling poachers to enter the park without resistance (Martin, 2004; Martin and Martin, 2006). The number of rhinoceros in Nepal has been increasing since 2005, given the improved park security associated with political stability in the country since that time (DNPWC, 2017). Achieving zero poaching for rhinoceros in Nepal since 2011 is an extraordinary accomplishment (Martin et al., 2013) that can be attributed to the Government's commitment and stakeholders' support towards the conservation of this iconic wildlife species (Acharya, 2016). Despite the recent success of rhinoceros conservation in both India and Nepal, poaching remains a major potential threat or risk to the ongoing conservation of rhinoceros (Martin and Vigne, 2012; Martin et al., 2013; DNPWC, 2017).

4.3. Rhinoceros population genetics needs further research

Our current understanding of rhinoceros genetics is not sufficient to guide rhinoceros population management for maintaining the highest possible level of genetic variability. Genetic diversity plays a vital role in evolutionary adaptation, which is crucial to the long-term survival of any species (Schemske et al., 1994). Previous studies have indicated that there is strong genetic differentiation between the Assam and

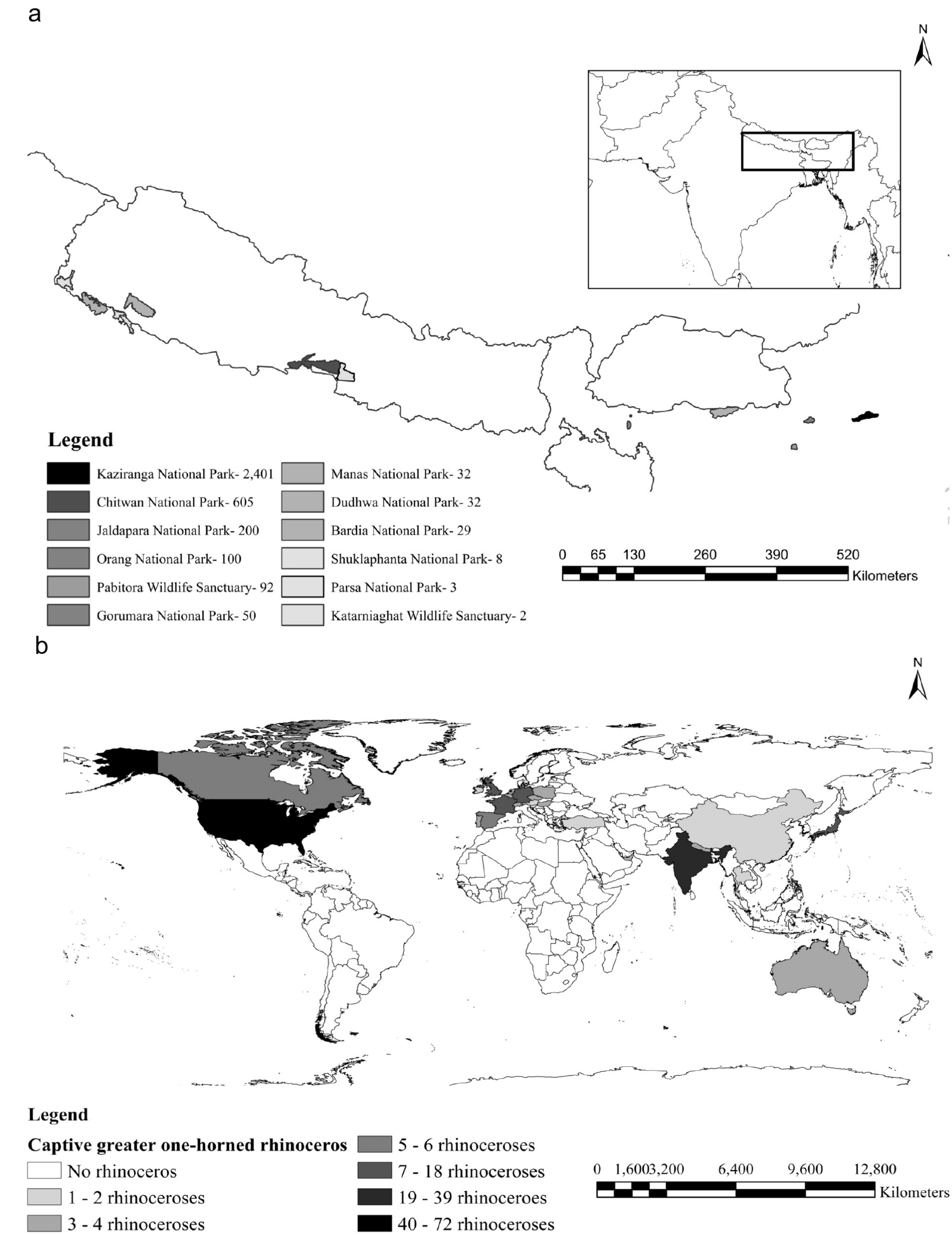

Fig. 7. Spatial distribution of greater one-horned rhinoceros, showing the current distribution of (a) free-ranging and (b) captive greater one-horned rhinoceros globally.

Nepal populations of rhinoceros (Zschokke and Baur, 2002). The extent of genetic divergence between these two remnant populations of rhinoceros suggests separate conservation programs are required, even for captive individuals, as long as the persistence of the entire species is not severely threatened (Zschokke et al., 2011). In addition to this, a significant level of genetic differentiation has been observed between the protected areas of Assam and West Bengal, especially Gorumara National Park, which showed a unique genetic signature. Given the degree of population genetic structure observed, prolonged separation of these protected areas is undesirable as this could lead to further loss of genetic diversity which could affect the long-term viability of the species (Das et al., 2015).

All captive rhinoceros descend from animals captured in one of the two large remaining populations in KNP, India and CNP, Nepal (Rookmaaker and Jones, 1998; Zschokke et al., 1998). These two populations have been separated for several centuries, and are slightly morphologically distinct (Groves, 1993). Both these populations have gone through a severe population bottleneck – the Indian population in 1908 and the Nepal population in 1962 (Zschokke, 2016). Bottlenecks are known to reduce genetic variability in a population and subsequently to increase susceptibility to inbreeding depression in the recovered population (Schemske et al., 1994). A study on inbreeding and outbreeding revealed that inbred individuals from the KNP population did not show reduced infant survival compared to those who were not inbred (Zschokke and Baur, 2002). In contrast, other studies have shown that offspring of matings between individuals from the KNP and the CNP populations had a much lower infant survival (58%) than non-outbred ones (82%), which suggests that the two populations might be partially genetically incompatible (Zschokke and Baur, 2002).

On the other hand, studies indicate that parity, not outbreeding, is responsible for infant mortality in the rhinoceros. These studies suggest that as CNP and KNP populations do not belong to separate subspecies, the union of wild and captive animals from CNP and KNP may help save the genetic diversity of the species (Pluhacek et al., 2007). This being said, while captive management of rhinoceros is healthy demographically, it is genetically limited (Foose and Wiese, 2006). Thus, it is worthwhile managing Indian and Nepal populations of rhinoceros separately until more is known about the genetic relationship. Further research on rhinoceros genetics should be undertaken to provide the knowledge required to maintain the highest genetic diversity possible in wild populations.

4.4. Population monitoring needs innovation

An analysis of the literature suggests that the population monitoring technique applied to rhinoceros in India and Nepal is limited to estimating minimum population size, and it does not provide the complete information required to manage the species properly. During the 1970s, photographs of individual rhinoceros were used to determine the minimum population size in Nepal (Laurie, 1978), and the block count method has subsequently been the most common approach for estimating rhinoceros population. This is a total count method that uses parallel strip transects to count and identify individual rhinoceros surveyed based on features such as horn shape, skin folds and body marks (Subedi et al., 2013; Borthakur et al., 2016; DNPWC, 2017). In India, rhinoceros population has been estimated using a similar total count method whereby rhinoceros are counted by observers riding elephants; multiple teams count the total number of individuals observed in assigned blocks, which are generally demarcated by physical boundaries such as rivers, streams or roads (Lahan and Sonowal, 1973). Unlike the block count method used in Nepal, the total count method adopted in India does not employ individual identification based on distinct body features (Borthakur et al., 2016).

A helicopter census of CNP in 1968 resulted in a figure of 81–108 rhinoceros; this was an underestimate since the population was at least 280 in 1977 (Martin, 1985). Rhinoceros counts from helicopter surveys underestimate the population because of poor visibility (Laurie, 1978; Kidwai et al., 2019). Since 2000, the population of rhinoceros in Nepal has also been enumerated every 4–5 years by the total count method, by observers riding tame elephants (Subedi et al., 2013). The presence of tall grass and closed-canopy forests in rhinoceros habitat make other methods of sample count impractical and inefficient (Lahan and Sonowal, 1973; Subedi et al., 2013). These total counts are similar to the aerial block counts used in Africa (Brockett, 2002; Kidwai et al., 2019).

However, the total count method is statistically unreliable (Cédric et al., 2016) and only provides the minimum population of the species inhabiting the area covered during the census (Lahan and Sonowal, 1973). Even with this limitation, the census of rhinoceros has been carried out for decades using this total count method, and no advanced scientific approach has been adopted for population estimation of the species (Borthakur et al., 2016). Studies suggest that there is a need to increase monitoring efforts and to get spatially explicit information on rhinoceros and habitat using robust analytical tools in order to make more confident predictions about the rhinoceros' future (Cédric et al., 2016). Genetic monitoring may also provide the information required for various aspects of population dynamics, and it is feasible to estimate the population of rhinoceros in the wild using a non-invasive genetic approach that extracts viable DNA from dung samples (Borthakur et al., 2016). Given the shortfalls of current monitoring methods and the availability of new ecological and genetic approaches, there is potential for an innovative approach to monitoring populations of rhinoceros in the wild that combines traditional and advanced ecological and genetic monitoring techniques. This approach would provide the necessary data for the long-term conservation of the species.

5. Conclusion

Our review of rhinoceros literature over the last three decades revealed that there are >200 peer-reviewed articles published on a wide range of themes. The majority of the studies were related to rhinoceros biology, and there were no studies on likely impacts of the changing climate on rhinoceros and its habitat. Other areas with research gaps include population genetics, disease, and habitat dynamics. In the last five years, the biology of the rhinoceros remains the primary focus of the research, but there is a growing interest in population and habitat dynamics, and rhinoceros genetics. Based on our analysis, further research in the following areas is required:

a. Long-term experimental research on rhinoceros and its habitat dynamics including density-dependent effects that can provide valuable information required for securing the future of rhinoceros; predominantly in the context of threats that arise from invasion of prime grassland habitat by exotic weeds and woodlands; and drying up of wetlands in rhinoceros habitat, and other emerging threats associated with the impacts of global climate change on rhinoceros habitat.
b. Vulnerability assessments of rhinoceros help to identify critical factors likely to pose threats to small and isolated populations. Such assessments also help to identify key areas of intervention that would help to minimize the likely adverse impacts of climate change on rhinoceros and its habitat.
c. The development of innovative population monitoring techniques to generate detailed information on spatial and temporal distribution of the rhinoceros. This is not only crucial for maintaining a viable population of rhinoceros in the context of ongoing threats but is also important to provide insights on population dynamics. These insights are essential to understand the likely impacts of climate change on rhinoceros and its habitat.
d. A detailed investigation on rhinoceros genetics that can provide vital information on possible ways for maintaining a healthy population both in captivity and wild, as species which are genetically diverse are less prone to extinction and more resistant to the adverse impacts of climate change.
e. Research on rhinoceros movement outside the protected areas with particular reference to human-rhinoceros conflict and its mitigation, and the analysis of the current and future habitat suitability outside the protected areas in India and Nepal that can provide vital information for maintaining the long-term viability of the rhinoceros in the human-dominated landscape.
f. Studies of the impacts of both ongoing and planned tourism

activities, and other socio-economic developments in and around rhinoceros habitat, as some of these activities are likely to further fragment and degrade the rhinoceros habitat which is already small and fragmented into isolated patches of protected areas extending over India and Nepal.

The rhinoceros is an iconic species that relies on effective management for its persistence in both India and Nepal. Through the implementation of the aforementioned research programs, we believe that this flagship species will have a greater chance of persistence well into the future.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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