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SYNTHESIS & INTEGRATION

Quantitative models of *Rhipicephalus* (*Boophilus*) ticks: historical review and synthesis

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Abstract. Several tick species, in what is now known as the subgenus *Boophilus* in the genus *Rhipicephalus*, are economically important ectoparasites of livestock and other ungulates; as vectors of pathogens that kill cattle, they remain among the most studied ticks in the world. Researchers have developed quantitative computer models of *Rhipicephalus* ticks since the early 1970s to study complex biological and ecological relationships that influence management or eradication of ticks and tick-borne diseases. We review the 45-yr history of *Rhipicephalus* (*Boophilus*) models, which were developed and applied first in Australia, 10 yr later in North and South America, then soon after in Africa. Models progressed from analytical models of a portion of tick life cycles, to simulation models of complete life cycles or ecoclimatic indices, to the current emphasis on GIS-based bioclimatic envelope models estimated from remotely sensed data and tick presence records. Earlier models were used primarily to predict effects of management techniques, such as use of sterile hybrid ticks, pasture rotation, acaricides, vaccines, and resistant cattle, while more recent models have been used to predict the potential for range expansion, especially due to global climate change and wildlife hosts, as well as in the face of competition with other tick species. We summarize characteristics of these models and compare those of population dynamics and bioclimatic envelope models. We discuss the past and present utility of these models and provide a perspective on future *Rhipicephalus* (*Boophilus*) modeling efforts.

Key words: analytical model; cattle tick; *Rhipicephalus* (*Boophilus*) *annulatus; Rhipicephalus* (*Boophilus*) *australis; Rhipicephalus* (*Boophilus*) *decoloratus; Rhipicephalus* (*Boophilus*) *microplus;* simulation model.

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INTRODUCTION

The subgenus *Boophilus*, genus *Rhipicephalus* (Acari: Ixodidae), contains six currently recognized species of ticks that primarily parasitize ungulates (Guglielmone et al. 2014): *Rhipicephalus annulatus*, *R. australis*, *R. decoloratus*, *R. geigyi*, *R. kohlsi*, and *R. microplus*. All six species are multivoltine (more than one generation per year) and exhibit a one-host life history (larvae, nymphs, and adults feed and develop on a single host) that is followed by oviposition, incubation, and larval life in off-host habitats (Murrell and Barker 2003, Nicholson et al. 2009). *Rhipicephalus decoloratus* (Koch) is distributed in sub-Saharan Africa (Estrada-Peña et al. 2006*a*), while *R. geigyi* (Aeschlimann and Morel) has a narrow but wide east–west sub-Sahelian distribution from Senegal to Uganda, and *R. kohlsi*

(Hoogstraal and Kaiser) has a north–south distribution from Syria to Yemen (Kolonin 2009). *Rhipicephalus decoloratus* and *R. geigyi* tend to infest cattle, while *R. kohlsi* tends to infest sheep and goats. These three tick species have not appreciably expanded beyond their original distributions. In contrast, *R. annulatus* (Say) inhabits arid and temperate climates of the Mediterranean region to southern Russia, central Africa, parts of the Middle East, India, and Mexico (Estrada-Peña et al. 2006*a*, Kolonin 2009), and prior to 1943, it inhabited most of the southern United States (USA; Graham and Hourrigan 1977). *Rhipicephalus microplus* (Canestrini) originated in tropical climates of the Indian subcontinent and is now considered pan-tropical (George 1990, Estrada-Peña et al. 2006*a*). *Rhipicephalus australis* (Fuller), formerly considered a subspecies of *R. microplus* (Roberts 1970) but recently reinstated as a sibling species (Estrada-Peña et al. 2012), has Australasian, Southeast Asian, and Pacific Island distribution (Guglielmone et al. 2014). Mitochondrial genome sequences support the elevation of *R. australis* to species (McCooke et al. 2015) and indicate that *Rhipicephalus* (*Boophilus*) populations from southern China and northern India likely represent a cryptic species (Burger et al. 2014). Explorers, settlers, and soldiers of the 16th–20th centuries expanded the distributions of *R. microplus*, *R. australis*, and *R. annulatus* by moving infested cattle (Estrada-Peña and Salman 2013). It is estimated that 80% of the world's cattle population is exposed to parasitism by *R. microplus* or *R. australis* (de Castro et al. 1997).

Blood loss and irritation due to tick feeding cause direct losses of livestock reproduction, growth, and production of meat, milk, and draft services (Graf et al. 2004, de la Fuente et al. 2007). Additional indirect losses are caused by tick-transmitted pathogens, resulting in substantial morbidity and mortality (Graf et al. 2004, de la Fuente et al. 2007). For cattle within the range of *R. annulatus*, *R. microplus*, or *R. australis* populations, the main tick-borne pathogens are *Babesia bigemina* (Smith and Kilborne) and *Babesia bovis* (Babes), causal agents of bovine babesiosis, and *Anaplasma marginale* (Theiler), causal agent of anaplasmosis, each with significant economic impacts on cattle production (Estrada-Peña et al. 2006*a*). Consequently, these species have received much research attention in regions where they coincide with high cattle production, primarily Australia and the Americas.

The discovery that *R. annulatus* was responsible for transmitting *B. bigemina* from infected to noninfected cattle (Smith and Kilborne 1893) was followed by research and development of methods to control babesiosis by suppressing or eliminating tick populations (Graham and Hourrigan 1977). Control methods initially focused on farming/ranching practices of the period, but the discovery of acaricides and the plunge dip vat permitted large numbers of animals to be effectively treated if properly regulated (Graham and Hourrigan 1977). In the United States, systematic dipping of cattle in acaricides was found to effectively eradicate both *R. annulatus* and *R. microplus* from large regions. A national eradication program began in 1907 officially removed them from the United States by 1943, but emerging vulnerabilities along the U.S.–Mexico border in Texas have increased reintroductions of ticks and continuously threaten the southern United States (Racelis et al. 2012). Changes in land use, intergenerational land fractionation, a diversity of native and exotic hosts, changes in vegetation, and transboundary economic, social, and political issues risk compromising this hard-won biosecurity in the United States (Pérez de León et al. 2012). A similar zone exists in New South Wales, Australia (officially *R. australis*-free since 2004), along the fenced and monitored border it shares with the part of Queensland inhabited by *R. australis* (West 2005). Tick eradication programs in Australia became more difficult as *R. australis* acquired resistance to successive acaricide compounds from the 1930s (Angus 1996). Likewise, acaricide resistance contributed to the inability to eradicate *R. microplus* and *R. annulatus* from all parts of Mexico and *R. microplus* from Argentina (George et al. 2004). *Rhipicephalus australis* and *R. microplus* are recognized as two of the most pesticide-resistant arthropods in the world (Whalon et al. 2008).

Researchers took advantage of increasing computer power and availability in the 1970s to develop the first computer models of *Rhipicephalus* (*Boophilus*) life history and ecology. As research interests of laboratories in multiple countries shifted among tick life history, ecology, control, management, and eradication, models integrated field and laboratory data, predicted consequences of management strategies, and generated new hypotheses to be tested in future experiments or predicted in future models. In the current global context, modeling can be used to study interactions between behavior of cattle and deer (or other wildlife species) in tick-infested landscapes, identify dynamic relationships between host diversity and tick dispersal and maintenance, and improve tactics to suppress or eliminate ticks; these aspects have been identified as gaps in the ability to develop effective strategies to control ticks affecting livestock and wildlife (Morgan et al. 2004). Moreover, predicting future impacts of climate oscillations and perturbations by modeling normal and extreme conditions would better inform regulatory officials and policy makers about operational needs and regulatory changes, as suggested for other disease systems influenced by global change (Anyamba et al. 2012).

Herein, we first provide a chronology of quantitative models developed to simulate either population dynamics or the "bioclimatic envelope" (Araújo and Peterson 2012) of *Rhipicephalus* (*Boophilus*) ticks; it demonstrates how models (1) evolved over time to address new research topics and (2) propagated throughout the global research community. We then categorize the models by mathematical structure and output; compare and contrast their structures, data, and dynamics; and suggest how and what kinds of models can complement future research and applications to decrease negative effects of tick parasitism; increase food security; and promote agricultural, environmental, and social stability and sustainability. We limited the review to references in the scientific literature that describe new model structure, evaluation, or predictions in some detail, which resulted in 101 references describing 113 model instances (Tables 1–4, Figs. 1, 2; Appendix S1: Fig. S1). This review is similar to one performed on the modeling of tick-borne pathogens carried mainly by *Ixodes ricinus* (L.) ticks (Norman et al. 2016).

CHRONOLOGY OF *RHIPICEPHALUS* (*BOOPHILUS*) MODELS

Australian initiation (1973–1989)

In 1973, researchers from Australia's Commonwealth Scientific and Industrial Research Organization (CSIRO) developed the first model explicitly representing *Rhipicephalus* ticks (Sutherst et al. 1973), an analytical model predicting on-host mortality of *Rhipicephalus australis*. The following year, they introduced the TICK1 simulation model, with a weekly time step (Sutherst and Dallwitz 1979). By 1980, they had produced an analytical model (PICKUP) that predicted larval host finding (Sutherst et al. 1978), added additional driving variables to their model of on-host mortality (Sutherst et al. 1979*b*), and began to develop TICK2, a more detailed simulation model with a daily time step (Maywald et al. 1980).

In the late 1970s, they also produced a Leslie matrix model of *R. australis* population dynamics (MATIX) to simulate integrated tick-management strategies (Sutherst et al. 1979*a*), including those for crossbred cattle (Sutherst et al. 1980*a*, *b*). They also combined MATIX with models of population genetics to evaluate development of acaricide resistance (Sutherst and Comins 1979) and with decision-analysis models (Elder et al. 1983, Norton et al. 1983, 1984, Elder and Morris 1986) to predict effects of management strategies. They developed a model to predict off-host larval mortality (LARVS; Utech et al. 1983) and then combined it with their model of on-host mortality (Bourne et al. 1988). They also developed a model of interspecific competition (STERHB) between *Rhipicephalus microplus* and *Rhipicephalus decoloratus*, the first *Rhipicephalus* model applied to Africa (Sutherst 1987*a*). By 1987, their TICK2 model, the first simulation model of ticks to have a daily time step, was operational; it also represented each cow individually (Dallwitz 1987*a*, *b*, *c*).

In 1985, they introduced CLIMEX, a bioclimatic envelope model that predicted an "ecoclimatic index" for a species' population at a given geographic point as a function of indices of potential growth and stress (Sutherst and Maywald 1985). CLIMEX was used to predict distributions of *R. australis* in southern Australia and *R. microplus* in southern Africa (Sutherst 1987*b*); to analyze climate-change effects on tick distribution (Maywald and Sutherst 1989); and, when integrated into an expert system, to help agricultural advisors recommend tick-management strategies (Sutherst and Bottomley 1989).

Table 1. Chronological list of 76 references that include 79 population dynamics models of *Rhipicephalus* (*Boophilus*) ticks, indicating key reference and model characteristics.

				Reference char.¶				Model characteristics#						
References	Location of system modeled†	Sp.‡	Type§	D	SA	P	E	S	A	Name	Lang.	Time step‖	Max. time span‖	Overall spatial scale
Sutherst et al. (1973)	AU	au	P	●	–	●	●	–	●	–	–	–	–	Cow
Sutherst and Dallwitz (1979)	Qld., AU	au	C	●	●	●	●	–	–	–	Fortran	1 w	35 mo	Ranch
Sutherst et al. (1978)	AU	au	P	●	●	●	–	–	●	PICKUP	–	1 d	50 d	Pasture
Sutherst et al. (1979*a*)	Qld., AU	au	C	●	●	●	●	–	–	MATIX	Fortran	1 w	1 y	Ranch
Sutherst et al. (1979*b*)	AU	au	P	–	–	●	–	–	●	–	–	1 gn		Cow
Sutherst and Comins (1979)	AU	au	P	●	●	●	–	–	●	–	–	1 gn	4 gn	Pasture
Sutherst et al. (1980*b*) (‘79)	Qld., AU	au	C	–	–	●	–	–	–	MATIX	Fortran	1 w	1 y	Ranch
Sutherst et al. (1980*a*) (‘79)	Qld., AU	au	C	–	–	●	–	–	–	MATIX	Fortran	1 w	1 y	Ranch
Maywald et al. (1980)††	Qld. and NSW, AU	au	C	●	–	●	●	–	–	TICK1	Fortran	1 w	30 mo	Pasture
Maywald et al. (1980)††	Qld., AU	au	C	●	●	●	–	–	–	MATIX	Fortran	1 w	4 y	Pasture
Maywald et al. (1980)††	AU	au	C	●	–	–	–	–	–	TICK2	Fortran	1 d	1 y	Ranch
Osburn and Knipling (1982)	US	m, an	P	–	–	●	–	–	–	–	–	3 mo	21 mo	4000 ha
Elder et al. (1983)	Qld., AU	au	C	–	–	●	–	–	–	MATIX	–	–	–	Ranch
Norton et al. (1983)	AU	au	C	●	●	●	–	–	–	MATIX	–	1 w	eq.	Ranch
Smith (1983)	–	m	P	●	–	●	–	–	–	–	Basic	3 mo	eq.	Pasture
Utech et al. (1983)	Qld., AU	au	P	–	–	●	●	–	–	LARVS	–	1 d	3 mo	Pasture
Weidhaas et al. (1983)	US	b	C	●	–	●	–	–	–	–	Fortran	1 w	21 mo	Pasture
Smith (1984)	–	m	–	–	●	–	–	–	–	–	–	–	–	–
Smith et al. (1984)	BR/UY	m	P	–	–	●	●	–	–	–	Basic	3 mo	eq.	Pasture
Norton et al. (1984)	Qld., AU	au	C	●	●	●	–	–	–	–	–	1 w	4 y	1–2 pastures
de la Vega and Díaz (1985*a*, *b*, *c*)	Cuba	m	P	–	–	●	–	–	●	–	–	1 d	d → fh	♀ & eggs
de la Vega and Díaz (1986)	Cuba	m	P	–	–	●	●	–	●	–	–	1 d	d → fh	♀ & eggs
Elder and Morris (1986)	Qld., AU	au	C	–	●	●	–	●	–	–	–	–	10 y	Ranch
Dallwitz (1987*a*, *b*, *c*)	AU	au	C	●	–	–	–	●	–	TICK2	Fortran	1 d	–	Ranch
de la Vega and Díaz (1987)	Cuba	m	P	–	–	●	–	–	●	–	–	1 d	3 mo	Larval cohort
Sutherst (1987*a*)	Africa	m, d	P	●	–	●	–	–	–	STERHB	–	1 gn	10 gn	Range overlap
Bourne et al. (1988)	AU	au	P	●	–	●	–	–	●	–	–	1 w	4.5 y	Ranch

(Table 1. *Continued*)

				Reference char.¶				Model characteristics#						
References	Location of system modeled†	Sp.‡	Type§	D	SA	P	E	S	A	Name	Lang.	Time step‖	Max. time span‖	Overall spatial scale
de la Vega et al. (1988)	Cuba	m	P	●	–	●	–	–	●	–	–	1 d	43 d	2 pastures
Smith (1989, 1991)	BR/PY	m	P	●	–	●	–	–	–	–	MS Works	1 w	eq.	Pasture
Popham and Garris (1991, 1989)	Puerto Rico, US	m	C	●	–	●	–	●	–	–	–	1 d	1000 d	33 ha
Höner and Gomes (1990)	BR	m	–	–	–	–	–	–	–	degree–day	–	1 d	–	Country
Mount et al. (1991)	Americas/ AU	m, an	C	●	–	●	●	–	–	BCTSIM	Basic	1 w	3 y	World
Strey et al. (1991)	Texas, US/MX	an	P	●	–	●	●	–	●	–	SAS	1 d	141 d	Egg mass
de la Vega and Díaz (1992)	Cuba	m	P	–	–	●	–	–	●	–	–	1 d	68 d	2 pastures
Haile et al. (1992)	Americas/ AU/Africa	m, an	C	●	–	●	●	–	–	BCTSIM	Basic	1 w	>5 y	World
de la Vega et al. (1993)	Cuba	m	P	●	–	●	–	–	–	DESPOBLE	–	1 d	140 d	Egg mass
Höner et al. (1993)††	SC, BR	m	C	–	–	●	–	–	–	BCTSIM	Basic	1 w	–	Pasture
Höner et al. "(1993)††	SC, BR	m	–	–	–	●	–	–	–	Agro_ degree_day	–	1 d	1 y	Pasture
Arantes et al. (1995)	MG, BR	m	–	–	–	●	–	–	–	BRAMATIX	–	1 d	1 y	Ranch
Saueressig and Höner (1995)	Federal District, BR	m	–	–	–	●	–	–	–	Agro_ degree_day	–	1 d	–	Pasture
Floyd et al. (1995)	Qld., AU	au	C	–	●	●	●	–	–	TICK2	Fortran	1 d	5 y	Ranch
Lodos et al. (1995)	Cuba/ BR	m	C	●	–	●	●	–	–	TICKSIM	C++	1 w	1 y	Pasture
Rodríguez (1995)	Cuba	m	C	●	–	–	–	–	●	–	–	1 w	33 w	Cow
Labarta et al. (1996)	Cuba	m	C	–	–	●	●	–	–	–	Pascal	1 w	1 y	Cow
Teel et al. (1996)	Texas, US/MX	b	C	●	●	●	–	–	–	–	STELLA	1 d	720 d	1000 ha
Hall et al. (1996)	AU	au	C	●	–	●	●	–	–	TICK1	Fortran	1 d	1 y	Continent
Sutherst et al. (1996)	AU	au	C	–	–	●	–	–	–	TICK1	–	–	–	Continent
Dixon et al. (1997)	Qld., AU	au	C	●	●	●	–	–	●	–	Matlab	1 w	1 y	Pasture
Abramson et al. (1997)	AU	au	C	●	–	●	–	–	–	TICK1	Fortran	1 w	10 y	Continent
Teel et al. (1997)	Texas, US/MX	b	C	–	–	●	–	–	–	–	STELLA	1 d	5 y	800 ha
Beugnet et al. (1998)	NC	au	C	●	●	●	–	–	–	–	–	3 w	3 y	150 ha
Teel et al. (1998)	Texas, US/MX	b	C	–	–	●	–	–	–	–	STELLA	1 d	2 y	800 ha
Basher (1998)	AU	au	C	–	–	●	–	–	–	TICK1	–	–	1 y	Continent
Lodos et al. (1999)	Cuba/BR/MX	b	C	●	●	●	●	–	–	TICKSIM	C++	1 w	3 y	Pasture
Sutherst et al. (1999)	Qld., AU	au	C	●	–	●	●	–	●	–	–	1 d	d → fh	Egg mass

(Table 1. *Continued*)

				Reference char.¶				Model characteristics#						
References	Location of system modeled†	Sp.‡	Type§	D	SA	P	E	S	A	Name	Lang.	Time step‖	Max. time span‖	Overall spatial scale
Smith et al. (1999, 2000)	BR/UY	m	–	●	–	●	–	–	–	–	MS Works	1 w	2 y	Herd
Hernández-Arrieta et al. (2000)	VZ	m	C	●	–	●	–	–	–	–	STELLA	1 d	3 y	Ranch
Lodos et al. (2000)	Cuba/BR	m	C	●	●	●	●	–	–	TICKSIM	C++	1 w	8 mo	Pasture
Fonseca et al. (2000)	MG, BR	m	C	–	–	●	●	–	–	BCTSIM	Basic	1 w	1 y	Pasture
Sutherst (2000)	Qld., AU	au	C	–	–	●	–	–	–	TICK2	–	–	–	–
Sutherst et al. (2000)	Qld., AU	au	C	–	●	●	–	–	–	TICK2	–	–	eq.	Pasture
Corson et al. (2001)	Texas, US/MX	b	C	●	–	●	–	–	–	–	STELLA	1 d	1190 d	800 ha
Sutherst (2001)	Qld., AU	au	C	–	–	●	●	–	–	TICK1/2	–	–	2 y	Herd
Estrada-Peña (2002)	sub-Saharan Africa	d	C	●	●	●	●	–	–	BDM	ERDAS Imagine	10 d	16 y	64 km^2
Delgado (2002)	MG, BR	m	C	–	–	●	●	–	–	BCTSIM	–	–	–	–
Corson et al. (2003)	Texas, US	b	C	–	–	●	–	●	–	–	STELLA	1 d	2 y	800 ha
Teel et al. (2003)	Texas, US	b	C	●	●	●	–	●	–	–	STELLA	1 d	2 y	100 ha
White et al. (2003)	AU	au	C	●	●	●	–	–	–	TICK1	–	1 w	1 y	Continent
Corson et al. (2004)	Texas, US	b	C	●	●	●	●	●	–	BoopMod	STELLA	1 h	2 y	Pasture
Estrada-Peña et al. (2006*b*)	NE AR	m	C	–	–	●	–	●	–	BoopMod	Fortran	1 h	10 y	Region
Zeman and Lynen (2010)	TZ	m, d	C	●	●	●	●	–	–	–	–	unitless	eq.	2500 deme cells
Merino et al. (2011)	Tmp., MX	m	C	–	–	●	●	●	–	–	Simgua	1 d	1000 gn	Cattle
Miller et al. (2012)	Texas, US	an	C	–	–	●	–	●	–	–	–	1 d	10 y	Region
Estrada-Peña et al. (2014)	NE MX	b	C	●	–	●	●	–	–	–	–	10 d	5 y	Region
Wang et al. (2016)	Texas, US	m	C	●	●	●	●	●	–	–	NetLogo	1 w	7 y	900 ha

Note: The symbol "●" signifies "yes/present," while "–" signifies "no/absent."

† Location: AU, Australia; BR, Brazil; MG, Minas Gerais; MX, Mexico; NC, New Caledonia; NSW, New South Wales; Paraguay, PY; Qld., Queensland; SC, Santa Catarina; Tmp., Tamaulipas; TZ, Tanzania; UY, Uruguay; US, United States; VZ, Venezuela.

‡ Species represented: au, *R. australis*; m, *R. microplus*; an, *R. annulatus*; d, *R. decoloratus*; b, merged *R. microplus/annulatus.*

§ Type of model: P, portion of life cycle; C, complete life cycle.

¶ Reference characteristics: D, describe model details (equations); SA, perform sensitivity analysis; P, make predictions; E, evaluate model accuracy.

Model characteristics: S, stochastic; A, analytical; Lang., language or software.

‖ Time step and time span: m, minute; d, day; w, week; mo, month; gn, generation; y, yr; d→fh, drop to first hatch; d→ll, drop to last larva; eq., equilibrium.

†† Multiple models described in one reference.

Table 2. Chronological list of 76 references that include 79 population dynamics models of *Rhipicephalus* (*Boophilus*) ticks, indicating key model content.

	Stages†					Drivers‡					Management§						Factors¶					Other#	
References	PO	O	E	FL	OL	T	H	P	Ev	SM	PS	RG	AT	C	V	EA	HR	AR	HF	CC	TD	*B*	S
Sutherst et al. (1973)	–	–	–	●	●	–	–	–	–	–	–	–	–	–	–	–	●	–	–	–	–	–	–
Sutherst and Dallwitz (1979)	–	●	●	●	●	●	●	–	–	●	●	–	●	–	–	–	●	●	●	–	–	–	–
Sutherst et al. (1978)	–	–	–	●	–	–	–	–	–	–	●	–	–	–	–	–	–	–	●	–	–	–	–
Sutherst et al. (1979*a*)	–	●	●	●	●	–	–	–	–	–	●	●	●	–	–	●	●	●	–	–	–	–	–
Sutherst et al. (1979*b*)	–	–	–	●	●	–	–	–	–	–	–	–	–	–	–	–	●	–	–	–	–	–	–
Sutherst and Comins (1979)	–	–	–	–	●	–	–	–	–	–	–	–	●	–	–	●	●	●	–	–	–	–	–
Sutherst et al. (1980*b*)	–	●	●	●	●	–	–	–	–	–	–	–	●	●	–	–	●	–	–	–	–	–	–
Sutherst et al. (1980*a*)	–	●	●	●	●	–	–	–	–	–	●	–	●	●	–	●	●	●	–	–	–	–	–
Maywald et al. (1980)‖	–	●	●	●	●	●	–	●	●	–	●	–	●	–	–	–	●	●	●	–	–	–	–
Maywald et al. (1980)‖	–	●	●	●	●	–	–	●	–	–	●	●	●	–	–	●	●	●	●	–	–	–	–
Maywald et al. (1980)‖	●	●	●	●	●	●	●	–	–	–	●	●	●	●	–	●	●	●	●	–	–	–	–
Osburn and Knipling (1982)	–	–	–	●	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●
Elder et al. (1983)	–	–	–	–	–	–	–	–	–	–	●	●	●	–	–	●	●	–	–	–	–	–	–
Norton et al. (1983)	–	●	●	●	●	●	●	–	–	–	●	–	●	–	–	●	●	–	●	–	–	–	–
Smith (1983)	–	–	–	–	●	–	–	–	–	–	–	–	–	–	–	–	–	–	●	–	–	●	–
Utech et al. (1983)	–	–	–	●	–	●	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Weidhaas et al. (1983)	–	●	●	●	●	–	–	–	–	–	–	–	●	–	–	–	–	●	–	–	–	–	●
Smith (1984)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	–
Smith et al. (1984)	–	–	–	–	●	–	–	–	–	–	–	–	–	–	–	–	●	–	●	–	–	●	–
Norton et al. (1984)	–	●	●	●	●	–	–	–	–	–	●	–	●	–	–	●	●	●	●	–	–	–	–
de la Vega and Díaz (1985*a*, *b*, *c*)	●	●	●	–	–	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
de la Vega and Díaz (1986)	●	●	●	–	–	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Elder and Morris (1986)	–	–	–	–	–	–	–	–	–	–	●	●	●	–	–	●	–	–	–	–	–	–	–
Dallwitz (1987*a*, *b*, *c*)	–	–	●	●	●	●	–	●	●	●	–	●	●	●	–	–	●	●	●	–	–	●	–
de la Vega and Díaz (1987)	–	–	–	●	–	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sutherst (1987*a*)	–	–	●	●	●	–	–	–	–	–	–	–	●	–	–	–	●	–	●	–	–	–	●
Bourne et al. (1988)	–	–	–	●	●	●	–	–	–	–	–	–	–	–	–	–	●	–	–	–	–	–	–
de la Vega et al. (1988)	–	–	–	●	●	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Smith (1991)	–	–	–	–	●	–	–	–	–	–	–	–	●	–	–	–	–	–	●	–	–	●	–
Popham and Garris (1991)	–	●	●	●	●	●	●	–	–	–	–	–	●	–	–	–	●	–	–	–	–	–	–
Höner and Gomes (1990)	–	–	–	–	–	●	–	–	–	–	–	–	–	–	–	–	●	–	–	–	–	–	–
Mount et al. (1991)	●	●	●	●	●	●	●	–	–	–	–	–	–	–	–	–	●	–	–	–	–	–	–
Strey et al. (1991)	–	–	●	–	–	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
de la Vega and Díaz (1992)	–	–	●	●	●	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Haile et al. (1992)	●	●	●	●	●	●	●	–	–	–	–	–	–	–	–	–	●	–	–	–	–	●	–
de la Vega et al. (1993)	–	–	●	●	–	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Höner et al. (1993)‖	●	●	●	●	●	●	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Höner et al. (1993)‖	●	●	●	●	●	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Arantes et al. (1995)	–	–	–	–	●	–	–	–	–	–	–	–	●	–	–	–	–	–	–	–	–	–	–
Saueressig and Höner (1995)	●	●	●	●	●	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Floyd et al. (1995)	–	●	●	●	●	●	●	–	–	–	–	–	●	–	●	●	●	–	●	–	–	–	–
Lodos et al. (1995)	●	●	●	●	●	●	●	–	–	–	–	–	●	–	●	–	●	–	–	–	–	–	–
Rodríguez (1995)	–	●	●	●	●	–	–	–	–	–	–	–	–	–	●	–	–	–	–	–	–	–	–
Labarta et al. (1996)	–	●	●	●	●	–	–	–	–	–	–	–	●	–	●	–	–	–	–	–	–	–	–
Teel et al. (1996)	●	●	●	●	●	–	–	–	–	–	–	–	–	–	–	–	–	–	●	–	–	–	–
Hall et al. (1996)	●	●	●	●	●	●	●	–	–	–	–	–	●	–	●	●	●	–	●	●	–	–	–
Sutherst et al. (1996)	–	–	–	–	–	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dixon et al. (1997)	●	●	●	●	●	●	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Abramson et al. (1997)	–	–	–	●	●	●	●	–	–	●	–	–	●	–	●	●	–	–	–	–	–	–	–
Teel et al. (1997)	●	●	●	●	●	–	–	–	–	–	–	●	–	–	–	–	–	–	–	–	–	–	–
Beugnet et al. (1998)	–	–	●	●	●	–	–	–	–	–	–	–	●	–	–	–	●	–	●	–	–	–	–

(Table 2. *Continued*)

	Stages†					Drivers‡					Management§						Factors¶					Other#	
References	PO	O	E	FL	OL	T	H	P	Ev	SM	PS	RG	AT	C	V	EA	HR	AR	HF	CC	TD	*B*	S
Teel et al. (1998)	●	●	●	●	●	–	–	–	–	–	–	●	–	–	–	–	–	–	–	–	–	–	–
Basher (1998)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	–	–	–	●	–	–	–
Lodos et al. (1999)	●	●	●	●	●	●	●	–	–	–	–	–	●	–	●	–	●	–	–	–	–	–	●
Sutherst et al. (1999)	–	●	●	–	–	●	–	–	–	●	–	–	–	–	–	–	–	–	–	–	–	–	–
Smith et al. (1999, 2000)	–	–	–	–	–	–	–	–	–	–	–	–	●	–	–	–	–	–	–	–	–	●	–
Hernández-Arrieta et al. (2000)	●	●	●	●	●	●	–	–	–	–	–	●	–	–	–	–	●	–	●	–	–	–	–
Lodos et al. (2000)	●	●	●	●	●	●	●	–	–	–	–	–	●	–	●	–	●	–	–	–	–	–	–
Fonseca et al. (2000)	●	●	●	●	●	●	●	–	–	–	–	–	–	–	–	–	●	–	–	–	–	–	–
Sutherst (2000)	–	–	–	–	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sutherst et al. (2000)	–	–	–	–	●	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corson et al. (2001)	●	●	●	●	●	–	–	–	–	–	–	●	●	–	–	–	–	●	–	–	–	–	–
Sutherst (2001)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	–	–	–
Estrada-Peña (2002)	●	●	●	●	●	●	●	–	–	–	–	–	–	–	–	–	●	–	●	–	–	–	–
Delgado (2002)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	–
Corson et al. (2003)	●	●	●	●	●	–	–	–	–	–	●	●	–	–	–	–	–	–	–	–	●	–	–
Teel et al. (2003)	●	●	●	●	●	–	–	–	–	–	●	–	–	–	–	–	–	–	–	–	●	–	–
White et al. (2003)	–	–	●	●	●	●	●	–	–	●	–	–	●	–	–	●	●	–	●	●	–	–	–
Corson et al. (2004)	●	●	●	●	●	●	●	–	–	–	●	●	–	–	–	–	●	–	–	–	–	–	–
Estrada-Peña et al. (2006*b*)	●	●	●	●	●	●	●	–	–	–	●	–	–	–	–	–	●	–	–	–	–	–	–
Zeman and Lynen (2010)	–	–	–	–	–	●	–	●	–	–	–	–	–	–	–	–	●	–	–	–	–	–	●
Merino et al. (2011)	●	●	●	●	●	–	–	–	–	–	–	–	–	–	●	–	–	–	–	–	–	–	–
Miller et al. (2012)	●	●	●	●	●	●	●	–	–	–	–	–	–	–	●	–	–	–	–	–	–	–	–
Estrada-Peña et al. (2014)	●	●	●	●	●	●	●	–	–	–	–	–	–	–	●	–	–	–	●	–	–	–	–
Wang et al. (2016)	●	●	●	●	●	●	●	–	–	–	–	–	●	–	●	–	–	–	●	●	–	–	–

Note: The symbol "●" signifies "yes/present," while "–" signifies "no/absent."

† Stages: PO, female preoviposition; O, female oviposition; E, eggs; FL, free larvae; OL, on-host larvae.

‡ Drivers: T, air temperature; H, air humidity; P, precipitation; Ev, evaporation; SM, soil moisture.

§ Management: PS, pasture spelling; RG, rotational grazing; AT, acaricide treatment; C, culling; V, vaccination vs. ticks; EA, economic analysis.

¶ Factors: HR, host resistance; AR, acaricide resistance; HF, host finding; CC, climate change; TD, tick detection.

\# Other: *B*, *Babesia* spp.; S, sterile hybrid ticks.

‖ Multiple models described in one reference.

The Americas emerge (1982–1995)

Nearly 10 yr after *Rhipicephalus* models emerged in Australia, they began to appear in the Americas. Researchers from the U.S. Department of Agriculture, Agricultural Research Service (USDA-ARS), predicted effects of releasing sterile male hybrid (*Rhipicephalus annulatus* × *R. microplus*) larvae as an eradication strategy (Osburn and Knipling 1982). They later integrated much of this model into a more complex model that represented each life cycle stage explicitly (Weidhaas et al. 1983). Beginning at the same time, the original CSIRO model of on-host mortality was incorporated into the first simulation model of *Babesia bovis* to represent the vector population (Smith 1983, 1984); it was applied to sites in Brazil and Uruguay (Smith et al. 1984) and later transformed into a spreadsheet version (Smith 1991).

From 1985 to 1993, researchers from Cuba's National Center for Animal and Plant Health (CENSA) and the University of Havana (UH) published articles about modeling *R. microplus* in Cuba. They first built analytical degree-day models of preoviposition and incubation (de la Vega and Díaz 1985*a*, *b*, *c*, 1986), using them to predict effects of quarantine paddocks (de la Vega et al. 1988, de la Vega and Díaz 1992). They next built a degree-day model of larval longevity (de la Vega and Díaz 1987) and combined it with their previous model to predict the duration of the entire off-host phase (de la Vega et al. 1993). During the same period, researchers from the Brazilian Agricultural Research Corporation (EMBRAPA) predicted distribution of *R. microplus* at multiple sites in Brazil using CLIMEX alone (Saueressig and Honer 1993) or in combination with a degree-day

Table 3. Chronological list of 33 references that include 34 bioclimatic envelope models of *Rhipicephalus* (*Boophilus*) ticks, indicating key reference and model characteristics.

References	Location of system modeled†	Species‡	Reference characteristics§				Model characteristics¶				
			Desc.	SA	Pred.	Eval.	Analy.	Type	Calc.#	Spatial res.	Spatial extent
Sutherst and Maywald (1985)	world	au	●	–	●	–	–	CLIMEX	EI	Point	World
Sutherst (1987*b*)	SE AU/ZA	au/m‖	●	–	●	–	–	CLIMEX	EI	Point	Region
Sutherst and Maywald (1987)	Africa	m‖	–	–	●	–	–	CLIMEX	EI	Point	Continent
Sutherst and Bottomley (1989)	world	au/m	●	–	–	–	–	CLIMEX	EI	Point	World
Maywald and Sutherst (1989)	AU/ZA	au/m	●	–	–	–	–	CLIMEX	EI	Point	Continent
Höner and Gomes (1990)	BR	m	–	–	●	–	–	CLIMEX	EI	Point	Country
Höner et al. (1993)	S BR	m	–	–	●	–	–	CLIMEX	EI	Point	Region
Saueressig and Höner (1993)	S BR	m	–	–	–	–	–	CLIMEX	EI	Point	Region
Arantes et al. (1995)	Minas Gerais, BR	m	–	–	●	–	–	CLIMEX	EI	Point	Region
Saueressig and Höner (1995)	Federal District, BR	m	–	–	●	–	–	CLIMEX	EI	Point	Pasture
Sutherst et al. (1996)	AU	au‖	●	–	●	–	–	CLIMEX	EI	Point	Continent
Estrada-Peña (1999)	South America	m	●	–	●	●	●	GIS	cokriging	8 km	17.8×10^6 km^2
Cumming (2000)	Africa	m, an, d, g‖	●	–	●	–	●	GIS	GLM	¼°	Continent
Sutherst (2001)	eastern AU	au	–	–	●	–	–	CLIMEX	EI	Point	Region
Estrada-Peña (2001)	Central America	m	●	–	●	–	●	GIS	cokriging	–	Region
Cumming (2002)	Africa	m, an, d, g‖	●	–	–	–	●	GIS	GLM	¼°	Continent
Jubb and Campbell (2002)	Victoria, AU	au	–	–	●	–	–	CLIMEX	EI	Point	Local pastures
Estrada-Peña (2002)	sub-Saharan Africa	d	●	–	●	–	–	GIS	GLM	64 km^2	Region
Guglielmone et al. (2003)	NE AR	m	●	–	●	–	●	GIS	cokriging	8 km	13,039 km^2
Estrada-Peña (2003)	Africa	d‖	●	●	●		●	GIS	Gower	–	Continent
Fonseca et al. (2005)	RJ, BR	m	●	–	●	–	●	GIS	–	25 m	ca. 250 km^2
Estrada-Peña et al. (2005)	Americas	m	●	●	●	–	●	GIS	Gower	"°	Continent
Estrada-Peña et al. (2006*c*)	MX	m	●	–	●	–	●	GIS	Gower, ANOVA	8 or 100 km^2	Country
Estrada-Peña and Venzal (2006)	Texas, US/NE MX	m, an	●	●	●	●	●	GIS	climate	1.1 or 4 km^2	Region
Estrada-Peña et al. (2006*b*)	NE AR	m	●	●	●	–	●	GIS	Gower, ANOVA	6.25 km^2	Region
Rabiee et al. (2006)	NSW, AU	au	●	–	●	–	–	CLIMEX	EI	Point	Region

(Table 3. *Continued*)

References	Location of system modeled†	Species‡	Reference characteristics§				Model characteristics¶				
			Desc.	SA	Pred.	Eval.	Analy.	Type	Calc.#	Spatial res.	Spatial extent
Cumming and van Vuuren (2006)	world	m, an, d, g‖	●	–	●	–	●	GIS	GLM	317 km^2	World
Estrada-Peña and Venzal (2007)	Med.	an‖	●	–	●	–	●	GIS	ENFA	6.25 km^2	Region
Lynen et al. (2008)	Tanzania	m, d	●	–	●	–	●	GIS	ENFA	–	Country
Sutherst and Bourne (2009)††	Africa	m	–	–	●	–	–	CLIMEX	EI	Point	Subcontinent
Sutherst and Bourne (2009)††	Africa	m	●	–	–	–	●	GIS	GLM	Point	Subcontinent
De Clercq et al. (2013)	West Africa	m	●	–	●	●	–	Maxent	–	1 km^2	Region
Giles et al. (2014)	southern US	m, an	●	–	●	●	–	GARP, Maxent	–	1 km^2	Region
Phillips et al. (2014)	southern Texas, US	m	●	–	●	●	●	GIS	GLM	900 m^2	265 km^2

Note: The symbol "●" signifies "yes/present," while "–" signifies "no/absent."

† Location: AR, Argentina; AU, Australia; BR, Brazil; Med., Mediterranean; MX, Mexico; NSW, New South Wales; RJ, Rio de Janeiro State; US, United States; ZA, South Africa.

‡ Species represented: au, *R. australis*; m, *R. microplus*; an, *R. annulatus*; d, *R. decoloratus*; g, *R. geigyi*.

§ Reference characteristics: Desc., describe model details (equations); SA, perform sensitivity analysis; Pred., make predictions; Eval., evaluate model accuracy.

¶ Model characteristics: Analy., analytical; Calc., calculation method; spatial res., spatial resolution.

\# Calculation method: EI, ecoclimatic index; GLM, generalized linear model; Gower, Gower similarity; ANOVA, analysis of variance; ENFA, ecological niche factor analysis.

‖ Includes non-*Rhipicephalus* (*Boophilus*) tick species.

†† Multiple models described in one reference.

model (Honer and Gomes 1990, Saueressig and Honer 1995) or population dynamics model (Höner et al. 1993, Arantes et al. 1995).

In the United States, Popham and Garris (1991) developed a stochastic stage-structured transition matrix model of *R. microplus* to evaluate eradication strategies in Puerto Rico, while Strey et al. (1991) developed an analytical model of incubation of *R. annulatus* eggs. USDA-ARS researchers developed BCTSIM, which simulated the entire life cycle of *R. microplus* or *R. annulatus* (Mount et al. 1991) and later modified it to represent transmission of *Babesia* spp. by either tick species (Haile et al. 1992).

Australasia returns (1995–2006)

Several years of hiatus in tick model publishing in Australasia ended with the modification of TICK2 to represent vaccination against *R. australis* (Floyd et al. 1995). Later, Dixon et al. (1997) transformed BCTSIM into a stage-based transition matrix model to evaluate it with elasticity analysis, while Beugnet et al. (1998) created a matrix-based model to simulate control strategies for *R. australis* in New Caledonia.

TICK1 was revived to predict the influence of climate change on *R. australis* distribution in Australia and the latter's influence on beef cattle liveweight (Hall et al. 1996, Sutherst et al. 1996) and economic cost to the country's beef industry (Abramson et al. 1997, Basher 1998, White et al. 2003). Sutherst et al. (1996) also used CLIMEX to predict future ecoclimatic suitability for *R. australis* in Australia due to climate change. Commonwealth Scientific and Industrial Research Organization researchers later developed analytical models of egg production and hatching for inclusion in TICK1 (Sutherst et al. 1999), used TICK2 to simulate tick predation (Sutherst et al. 2000), and compared TICK2 predictions to observed tick counts on cattle (Sutherst 2000). They also used CLIMEX and TICK2 to predict distribution of *R. australis* and its on-host dynamics, respectively, in eastern Australia (Sutherst 2001). Jubb and Campbell (2002) used CLIMEX to predict *R. australis* habitat suitability

Table 4. Chronological list of 33 references that include 34 bioclimatic envelope models of *Rhipicephalus* (*Boophilus*) ticks, indicating key model content.

	Drivers†								Management‡						Factors§		Other¶	
References	TP	TA	T	H	R	NDVI¶	El	DL	LU	CD	PS	RG	AT	EA	HR	AR	CC	*B*
Sutherst and Maywald (1985)	●	–	●	–	●	–	–	●	–	–	–	–	–	–	–	–	–	–
Sutherst (1985, 1987*b*)	●	–	●	–	●	–	–	●	–	–	–	–	–	–	–	–	–	–
Sutherst and Maywald (1987)	●	–	●	–	●	–	–	●	–	–	–	–	–	–	–	–	–	–
Sutherst and Bottomley (1989)	●	●	●	–	●	–	–	●	–	–	–	–	●	–	●	–	–	●
Maywald and Sutherst (1989)	●	–	●	–	●	–	–	●	–	–	–	–	–	–	–	–	●	–
Höner and Gomes (1990)	●	–	●	–	●	–	–	●	–	–	–	–	–	●	●	●	–	–
Höner et al. (1993)	●	–	●	–	●	–	●	●	–	–	–	–	●	–	–	–	–	–
Saueressig and Höner (1993)	●	–	●	–	●	–	–	●	–	–	–	–	–	–	–	–	–	–
Arantes et al. (1995)	●	–	●	–	●	–	–	●	–	–	–	–	–	–	–	–	–	–
Saueressig and Höner (1995)	●	–	●	–	●	–	–	●	–	–	–	–	–	–	–	–	–	–
Sutherst et al. (1996)	●	–	●	–	●	–	–	●	–	–	–	–	–	–	–	–	●	–
Estrada-Peña (1999)	●	●	●	–	–	●	–	–	–	–	–	–	–	–	–	–	–	–
Cumming (2000)	●	–	●	–	●	●	●	–	–	–	–	–	–	–	–	–	–	–
Sutherst (2001)	●	–	●	–	●	–	–	●	–	–	–	–	–	–	–	–	–	–
Estrada-Peña (2001)	●	–	●	–	–	●	–	–	–	–	–	–	–	–	–	–	●	–
Cumming (2002)	●	–	●	–	●	●	●	–	–	–	●	–	–	–	●	–	–	–
Jubb and Campbell (2002)	●	–	–	–	–	–	–	●	–	–	●	–	–	–	–	–	–	–
Estrada-Peña (2002)	●	●	●	●	–	●	–	–	–	●	●	–	–	–	–	–	–	–
Guglielmone et al. (2003)	●	–	●	●	●	●	–	–	●	●	–	●	–	–	–	–	–	–
Estrada-Peña (2003)	●	–	●	●	–	●	●	–	–	–	–	–	–	–	–	–	●	–
Fonseca et al. (2005)	●	–	●	●	●	–	●	–	●	●	–	–	–	–	●	–	–	–
Estrada-Peña et al. (2005)	●	–	●	●	●	●	–	–	–	–	–	–	–	–	–	–	–	–
Estrada-Peña et al. (2006*c*)	●	●	●	●	●	●	–	–	–	–	–	–	–	–	–	–	–	–
Estrada-Peña and Venzal (2006)	●	–	●	–	–	●	–	–	–	●	–	–	–	–	–	–	–	–
Estrada-Peña et al. (2006*b*)	●	–	●	–	●	●	–	–	–	–	●	–	–	–	●	–	●	–
Rabiee et al. (2006)	●	–	●	–	●	–	–	●	–	–	–	–	–	–	–	–	–	–
Cumming and van Vuuren (2006)	●	–	●	–	●	–	–	–	–	–	–	–	–	–	–	–	●	–
Estrada-Peña and Venzal (2007)	●	–	●	–	●	●	–	–	–	–	–	–	–	–	–	–	●	–
Lynen et al. (2008)	●	●	●	●	●	●	–	–	–	–	–	–	–	–	–	–	●	–
Sutherst and Bourne (2009)#	●	–	●	●	●	–	–	●	–	–	–	–	–	–	–	–	●	–
Sutherst and Bourne (2009)#	●	–	●	●	●	–	–	–	–	–	–	–	–	–	–	–	●	–
De Clercq et al. (2013)	●	●	●	●	–	–	–	–	–	–	–	–	–	–	–	–	●	–
Giles et al. (2014)	●	●	●	–	●	–	–	–	–	–	–	–	–	–	–	–	●	–
Phillips et al. (2014)	●	–	●	●	●	●	–	–	●	–	–	–	–	–	–	–	–	–

Note: The symbol "●" signifies "yes/present," while "–" signifies "no/absent."

† Drivers: TP, tick presence; TA, tick absence; T, air temperature; H, air humidity; NDVI, Normalized Difference Vegetation Index; El, elevation; DL, daylength.

‡ Management: LU, land use; CD, cattle density; PS, pasture spelling; RG, rotational grazing; AT, acaricide treatment; EA, economic analysis.

§ Factors: HR, host resistance; AR, acaricide resistance.

¶ Other: CC, climate change; *B*, *Babesia* spp.

\# Multiple models described in one reference.

in Victoria, while Rabiee et al. (2006) spatially interpolated CLIMEX point predictions to predict risk of *R. australis* infestation in New South Wales.

Renewed efforts in the Americas (1995–2004)

During the same period, researchers from Cuba's Centro de Ingeniería Genética y Biotecnología (CIGB) used the model of Weidhaas et al. (1983) to predict effects of vaccination (with and without acaricide applications) on *R. microplus* populations in Cuba (Rodríguez 1995, Labarta et al. 1996). They then switched their base model to BCTSIM and adapted it to create a new model (TICKSIM) by modifying its vaccine submodel (Lodos et al. 1995, 2000) and adding a sterile-hybrid-release submodel (Lodos et al. 1999). Later, BCTSIM was recalibrated by

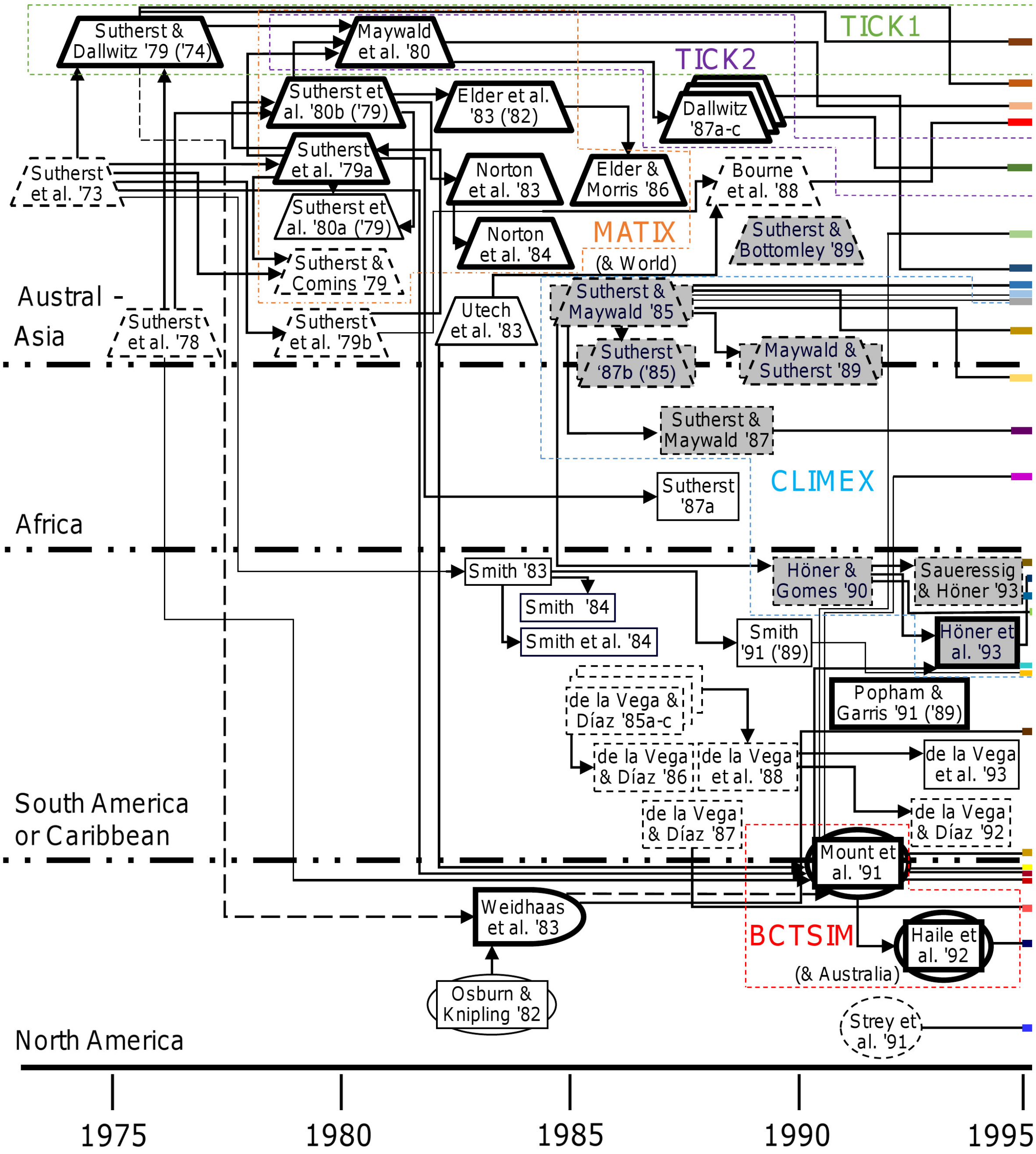

Fig. 1. *Rhipicephalus* (*Boophilus*)-model reference chronology and interconnections from 1973 to 1995, categorized by geographic region of application. Colors on arrows on the right edge identify connections to references in Fig. 2. Box shape represents species included (more than one possible): isosceles trapezoid, *R. australis;* rectangle, *R. microplus;* oval, *R. annulatus;* parallelogram, *R. decoloratus;* hexagon, three previous + *R. geigyi;* bullet, merged *R. microplus/annulatus*. Box outline represents type of model: dashed, analytical; solid, simulation. Thickness of outline represents how much life cycle simulated: thin, partial; thick, complete. Box shade represents model type: white, population dynamics; gray, bioclimatic envelope. Arrows represent borrowing: solid, equations or data; dashed, concepts. Tables 1–4 provide details about the models in these references.

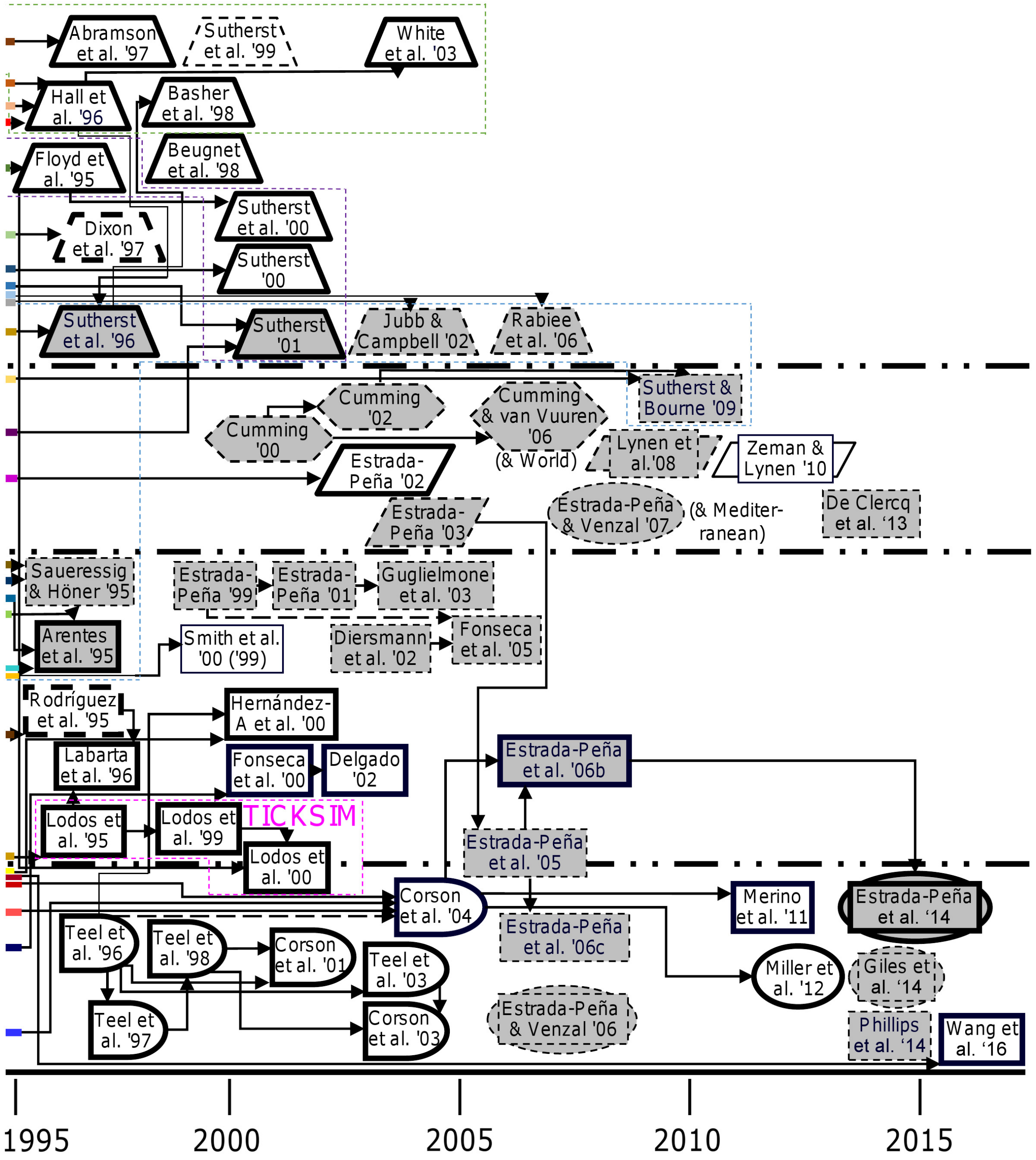

Fig. 2. *Rhipicephalus* (*Boophilus*)-model reference chronology and interconnections from 1995 to 2016, categorized by geographic region of application. Colors on arrows on the left edge identify connections to references in Fig. 1. Box shape represents species included (more than one possible): isosceles trapezoid, *R. australis;* rectangle, *R. microplus*; oval, *R. annulatus;* parallelogram, *R. decoloratus;* hexagon, three previous + *R. geigyi*; bullet, merged *R. microplus/annulatus*. Box outline represents type of model: dashed, analytical; solid, simulation. Thickness of outline represents how much life cycle simulated: thin, partial; thick, complete. Box shade represents model type: white, population dynamics; gray, bioclimatic envelope. Arrows represent borrowing: solid, equations or data; dashed, concepts. Tables 1–4 provide details about the models in these references.

Brazilian researchers to simulate *R. microplus* in Minas Gerais (Fonseca et al. 2000, Delgado 2002). Smith et al. (2000) used their spreadsheet model to analyze effects of tick-control strategies on enzootic stability of babesiosis in Brazil and Paraguay.

During this period, researchers from Texas A&M University (TAMU) developed a new model focusing specifically on daily habitat influences on *R. microplus* and *R. annulatus* populations in south Texas (Teel et al. 1996). They later adapted it to simulate rotational grazing strategies (Teel et al. 1997, 1998), acaricide treatments (Corson et al. 2001), and inspection of cattle for ticks under continuous (Teel et al. 2003) and rotational (Corson et al. 2003) grazing. Hernández-Arrieta et al. (2000) adapted the original TAMU model to simulate *R. microplus* in rotational grazing systems in Venezuela. Later, Corson et al. (2004) built a new simulation model (BoopMod) to predict influences of hourly microclimate, habitat heterogeneity, and within-pasture cattle movement. By this time, Sutherst (1998) had voiced concern: "The present situation, with parasitologists each doing their own thing in terms of developing and using software tools, is like the tower of Babel." It was a call for development of more generic approaches using common scientific terms and computer languages to facilitate communication and collaboration in the research and management of vector-borne diseases.

Rise of bioclimatic envelope models (1999–present)

Increasing availability of remote-sensing data throughout the 1990s helped shift *Rhipicephalus* research toward GIS-based bioclimatic envelope models (Araújo and Peterson 2012), which differed from mechanistic, physiologically based approaches such as CLIMEX. Initial studies focused on South America, predicting habitat suitability for *R. microplus* in South America (Estrada-Peña 1999), Central America (Estrada-Peña 2001), northeastern Argentina (Guglielmone et al. 2003), and Rio de Janeiro State, Brazil (Diersmann et al. 2002, Fonseca et al. 2005). Later studies predicted habitat suitability for *R. microplus* in the Americas from 1950 to 1999 (Estrada-Peña et al. 2005) and for *R. annulatus* and *R. microplus* along the Texas–Mexico border (Estrada-Peña and Venzal 2006), identified climate factors determining the latter's habitat suitability in Mexico (Estrada-Peña et al. 2006*c*), and predicted effects of climate change on habitat suitability for the latter in central Argentina, in combination with BoopMod to predict the probability of permanent populations (Estrada-Peña et al. 2006*b*).

During the same period, tick distributions were predicted for four *Rhipicephalus* (*Boophilus*) species (among many others) in Africa (Cumming 2000, 2002) and, in response to climate change, in the world (Cumming and van Vuuren 2006). Estrada-Peña (2002) predicted habitat suitability for *R. decoloratus* in sub-Saharan Africa but also built a population dynamics model of it driven by remotely sensed temperature and vegetation data. Estrada-Peña (2003) used remote-sensing data to predict habitat suitability for *R. decoloratus* (and three other species) in South Africa. Estrada-Peña and Venzal (2007) analyzed how climate influenced habitat suitability and ecological niche of *R. annulatus* (and five other species) in the Mediterranean region. Similarly, Lynen et al. (2008) predicted distribution ranges of *R. microplus* and *R. decoloratus* in Tanzania. Sutherst and Bourne (2009) repeated Cumming's 2002 study using only climate data and compared its predictions of range extensions of *R. microplus* in Africa due to climate change to those of CLIMEX. De Clercq et al. (2013) predicted climate suitability and distribution range of *R. microplus* in southern West Africa. Most recently, Giles et al. (2014) correlated *R. annulatus* and *R. microplus* presence and climate data in the southern United States, while Phillips et al. (2014) predicted south Texas habitats favorable to white-tailed deer (*Odocoileus virginianus* (Zimmerman)), a recognized host of *R. microplus* and *R. annulatus*, and habitats favorable to *R. microplus* larvae.

Return of population dynamics models (2010–present)

In a return to population dynamics models, Zeman and Lynen (2010) built Lotka–Volterra models of *R. decoloratus* and *R. microplus* competition in Tanzania, while Merino et al. (2011) used *R. microplus* data and BoopMod to predict effects of subolesin vaccination and RNAi on tick populations in Mexico. The following year, Miller et al. (2012) also used BoopMod to predict effects of vaccination on *R. annulatus* outbreaks in the Permanent Quarantine Zone of the U.S. Cattle Fever Tick Eradication Program. Estrada-Peña et al. (2014) predicted effects of white-tailed deer vaccination on *R. annulatus* and *R. microplus* in northeastern Mexico, while Wang et al. (2016) developed a spatially explicit, individual-based, stochastic *R. microplus* model for south Texas rangelands.

Comparison of References and Models

We summarize this large number of models by categorizing them by (1) "family" (if present), (2) tick species, and (3) mathematical structure and output. "Family" figuratively groups a given model and those adapted from it, often developed by the same or some of the same researchers. "Mathematical structure" distinguishes analytical models (i.e., temporal dimension ignored or implicit) from simulation models, whose explicit representation of the temporal dimension can capture additional interactions between variable environmental conditions and the phenology of tick life stages. "Output" distinguishes population dynamics models from bioclimatic envelope models. The choice and order of other distinguishing characteristics are arbitrary, but are based on over three decades of conversations between an acarologist and an ecological systems modeler. They range from generic (e.g., temporal and spatial scales, stochasticity) to increasingly tick-centric (e.g., representation of development, mortality, and fecundity) characteristics.

Model family

Due to the continual adaptation and application of pre-existing models, the 101 references necessarily described development and/or use of a smaller number of model families. Model families used most often include CLIMEX (15 refs), the family from TAMU (11 refs), MATIX (nine refs), TICK2 (eight refs), the family from CENSA/UH (eight refs), TICK1 (seven refs), Smith's *Babesia* model (five refs), and BCTSIM (five refs).

Rhipicephalus *(*Boophilus*) species included*

Of the 113 model instances, 70 (62%) represented *Rhipicephalus microplus* (41% exclusively so), probably due to its wider distribution than other *Rhipicephalus* (*Boophilus*) ticks, followed by 40 (35%) representing *Rhipicephalus australis* (33% exclusively so). Twenty-one model instances (19%) represented *Rhipicephalus annulatus* (only 3% exclusively so), nine (7%) represented *Rhipicephalus decoloratus* (only 3% exclusively so), and three (3%) represented *Rhipicephalus geigyi*. We found no models of *Rhipicephalus kohlsi*. Models of Weidhaas et al. (1983) and those from TAMU combined data for *R. microplus* (including *R. australis* at the time) and *R. annulatus* to create general *R. microplus/annulatus* models (bullet-shaped boxes; Figs. 1, 2).

Model mathematical structure and output

Most model instances were simulation models (69% of all instances) focused on population dynamics (56% of all instances). Before 1999, all analytical models focused only on population dynamics, while those published since 1999 focused more on the bioclimatic envelope. In the following paragraphs, we describe and compare in more detail models of the bioclimatic envelope (34 instances) versus those of population dynamics (79 instances).

*Characteristics of bioclimatic envelope models.—*Of the instances of bioclimatic envelope models, 44% used CLIMEX, 47% used analytical correlative species distribution models, and 6% used machine-learning models (Maxent). CLIMEX, which has been used for the longest time (since 1985), can represent habitat suitability for any poikilothermic species (Sutherst et al. 2007). Nietschke et al. (2007) contrasted CLIMEX to its successor DYMEX, which has a phenology component. CLIMEX appears to predict general population trends fairly well, but may be challenged by non-climate influences, such as biotic interactions, evolutionary change, and dispersal ability, as may all bioclimatic envelope models (Sinclair et al. 2010). Analytical and machine-learning models, which have become dominant (58% of all model instances since 2005), correlate tick presence/absence and presence only, respectively, with local climate characteristics, using a variety of approaches (e.g., logistic regression, multiple regression). In these models, factors such as Normalized Difference Vegetation Indices can serve as an approximation of local temperature and humidity. Olwoch et al. (2007) discussed positive and negative aspects of bioclimatic envelope models for *Rhipicephalus* ticks.

*Characteristics of population dynamics models.— 1. Temporal and spatial scales.—*Temporal and spatial scales of a model should be long enough and large enough, respectively, to encompass the main questions the model was developed to address, while the time step and spatial resolution should be short enough and small enough, respectively, not to overlook important functional and structural differences in the system modeled. When noted, most instances of population dynamics models followed a daily (35%) or weekly (32%) time step, although some had time steps as short as 1 h (Corson et al. 2004) or as long as one tick generation (~3–4 months; Sutherst et al. 1979*a*, Sutherst 1987*b*). Although TICK2 (Dallwitz 1987*a*) interpolated hourly temperatures from daily temperature data to drive development rates, BoopMod (Corson et al. 2004) was the first to simulate all processes at an hourly time step. Half of the instances of population dynamics models simulated periods ≤2 yr (51%), though continuous time spans ranged from 43 days (Sutherst et al. 1978, de la Vega et al. 1988) to 1000 generations (Merino et al. 2011). Spatial scales of these models also varied greatly. Most encompassed a ranch or single- or multi-pasture area (57%), but spatial scale ranged from a single egg mass (de la Vega et al. 1993) to multiple locations in the world (Haile et al. 1992). To represent infestations at large scales, 12 instances of population dynamics models were applied to multiple point locations to predict potential geographic distribution of ticks.

*2. Stochasticity.—*Stochasticity should be included in models when it is important to represent explicitly inherent variability in the system being modeled and/or uncertainty associated with estimates of model parameters. On the other hand, stochasticity makes the models more difficult to analyze and broadens the uncertainty in their predictions. Hence, only 15% of the population dynamics models contained stochastic variables, representing factors such as *Babesia* transmission (Dallwitz 1987*b*), cattle price and season severity (Elder and Morris 1986), number of standard ticks on cows (Corson et al. 2003, Teel et al. 2003), and habitat preferences (Corson et al. 2004). Sutherst (1983) recommended "stochastic elements to provide probabilities of persistence as well as estimates of population size." The model of Popham and Garris (1991) included more stochastic variables than any other model, with probability density functions for development and mortality rates and normally distributed sex ratios and host resistance levels.

*3. Model structure.—*Only 20% of the population dynamics models had an analytical structure. Some authors integrated these analytic models into existing simulation models (Utech et al. 1983, Sutherst et al. 1999), while others created simulation models to perform analytical calculations (e.g., sum degree-days; de la Vega et al. 1993). Dixon et al.'s (1997) analytical transformation and elasticity analysis of BCTSIM (Mount et al. 1991) suggested that decreasing fecundity would increase effectiveness of control methods, something that no other model apparently had identified to that point.

*4. Weather.—*More than half of the population dynamics models (56%) represented temperature explicitly to drive processes within them. Some models included factors affecting egg development besides temperature, such as the development models of de la Vega and Díaz (1985*a*) and Strey et al. (1991). Most models used temperature to calculate development rates, though some models used temperature to calculate mortality rates (Utech et al. 1983, de la Vega and Díaz 1987) or host-finding rates (Mount et al. 1991, Haile et al. 1992, Hernández-Arrieta et al. 2000). Only 41% of the population dynamics models, representing mostly the model families of TAMU, TICK1, TICK2, and TICKSIM, explicitly included a measure of ambient moisture, usually as a stress factor influencing off-host mortality (Utech et al. 1983, Dallwitz 1987*a*). Factors used to represent ambient moisture in models included precipitation/evaporation (Sutherst and Dallwitz 1979, Sutherst and Maywald 1985, Dallwitz 1987*a*, Mount et al. 1991, Lodos et al. 1999), ambient relative humidity (Popham and Garris 1991), and saturation deficit (Utech et al. 1983, Mount et al. 1991, Haile et al. 1992, Lodos et al. 1999, Corson et al. 2004). All models that represented ambient moisture explicitly did the same for temperature. Finally, some population dynamics models were driven by GIS-based climate or vegetation data (Estrada-Peña 2002, Miller et al. 2012, Estrada-Peña et al. 2014, Wang et al. 2016).

All simulation models using ambient moisture explicitly, and most using temperature explicitly, ran with historical weather data. Ideally, models should use microclimate data to reflect the temperature and relative humidity ticks experience; among simulation models, only BoopMod (Corson et al. 2004) appears to have done so. Because use of meso- or macroclimate data may bias predictions of off-host development and mortality, researchers have tried to adjust these data for different habitat types to correct for possible biases (Mount et al. 1991, Haile et al. 1992).

The time step over which models aggregated weather data also influenced their results. As time step increases, weather fluctuations that may influence development and/or mortality rates become lost in a mean value. Sometimes, weather data existed at a temporal scale larger than the model's time step. For example, though running on a daily time step, some models (Popham and Garris 1991, Hernández-Arrieta et al. 2000) used monthly weather data without attempting to estimate daily fluctuations. In contrast, BCTSIM (Mount et al. 1991) estimated weekly weather from monthly weather, while TICK2 (Dallwitz 1987*a*) interpolated daily maximum and minimum temperatures to estimate hourly temperature.

*5. Development rates.—*Population dynamics models using temperature to drive development rates usually represented development as degree-days above a minimum developmental threshold (Sutherst and Dallwitz 1979, de la Vega and Díaz 1985*a*, Dallwitz 1987*a*, Mount et al. 1991, Strey et al. 1991). Others predicted development rates from field data (Sutherst et al. 1979*b*, Popham and Garris 1991), or as development periods that were fixed by season (Teel et al. 1996, Hernández-Arrieta et al. 2000) or independent of season (Weidhaas et al. 1983). In contrast, Popham and Garris (1991) used fixed probability density functions to simulate development from one stage to the next.

*6. Mortality rates.—*Population dynamics models represented mortality rates in similar fashions. All those that represented ambient moisture explicitly used it to influence mortality rates. BoopMod (Corson et al. 2004) estimated larval mortality rates as the sum of daily saturation deficit over a threshold. Sutherst and Dallwitz (1979) developed a unique method, using precipitation and evaporation to calculate a Soil Dryness Index that influenced egg mortality. Their model also included the influence of cold stress on egg mortality. Some models, however, used temperature alone to predict mortality rates (e.g., for larvae, de la Vega and Díaz 1987).

Some simulation models used both temperature and ambient moisture to influence mortality. BCTSIM (Mount et al. 1991) set off-host mortality rates for optimal conditions and modified them with indices of temperature, saturation deficit, and precipitation. In the probability density functions of Popham and Garris (1991), all off-host stages died at temperatures above 30°C or relative humidities below 30%, thresholds much lower than those used in any other model.

As with development rates, the remaining models fixed mortality rates by stage or season. Weidhaas et al. (1983) fixed weekly mortality rates regardless of season, while Osburn and Knipling (1982) did the same for larval mortality. Sutherst et al. (1979*b*), however, varied egg and larval mortality rates by season. Unlike all other models, TICK2 captured the greater sensitivity of young eggs to desiccation by decreasing a stress multiplier as eggs age (Maywald 1987). Estimated mortality rates influence the duration of life stages, including the one most important to managers: larval longevity. de la Vega and Díaz 1987 estimated last larval death from a cohort at 703 degree-days. Utech et al. (1983) calculated accumulated stress on questing larvae as a function of daily maximum temperature, though saturation deficit at 15:00 worked just as well. Their attempts to improve predictions of larval longevity by including soil moisture, minimum temperature, or precipitation were unsuccessful. On-host mortality rates in some models remained fixed during a simulation (Weidhaas et al. 1983, Teel et al. 1996), while others depended on cattle type and on-host tick density (Sutherst et al. 1973, Mount et al. 1991). Sutherst et al. (1979*a*) included the latter two variables and added a third, season.

*7. Fecundity.—*Population dynamics models had the same variety when simulating fecundity. Egg production remained constant for some (e.g., 3000/female; Weidhaas et al. 1983), but varied by season for others (e.g., 200–2000/female; Sutherst et al. 1979*b*). Popham and Garris (1991) varied egg mass size with values obtained from a normal distribution. Others represented egg production as a function of temperature (Sutherst and Dallwitz 1979) or of mean temperature during oviposition and cattle type (Mount et al. 1991). Most models representing eggs assumed a 1:1 female-to-male sex ratio for them, but a few (Mount et al. 1991, Hernández-Arrieta et al. 2000, Corson et al. 2004) used the more precise value of 1.36:1 (Davey and Cooksey 1988) once it became available.

8. *Host encounter rate.—*Most population dynamics models used a constant host-larvae encounter rate (Sutherst and Dallwitz 1979, Sutherst et al. 1979*a*, Weidhaas et al. 1983, Teel et al. 1996) or varied the rate by season (Sutherst et al. 1979*b*). Popham and Garris (1991) again used a probability density function to represent larval encounter. Others, however, explicitly included the influence of other factors. For example, Mount et al. (1991) varied encounter rate as a function of host density, ambient temperature, and larval density, which provided negative feedback on encounter rate. The complex encounter-rate model of Sutherst et al. (1978), PICKUP, required estimates of host density, larval density, mean cow speed, and width of area swept per cow to predict the encounter rate. TICK2 appeared to use the same method (M. J. Dallwitz, *personal communication*). Most models defined encounter rate with a single variable that represented both spatial encounter of the grazing host with larvae and the number or proportion of larvae picked up. In contrast, models from TAMU represented encounter rate and pickup rate separately.

Geographic Summary

Models in Australia tended to focus first on farm-level management techniques such as pasture “spelling” (i.e., excluding grazing to increase ground cover and forage quality) and acaricide use, and then on climate-driven bioclimatic envelope models (i.e., CLIMEX). Models in South America first focused on duration of the off-host phase and then bioclimatic envelope models and effectiveness of anti-tick vaccines. Those in North America first focused on release of sterile hybrid males, then complex cattle-tick-landscape models focusing on eradication, then a combination of GIS-based bioclimatic envelope models and cattle-tick-landscape models focusing on control and/or management. Models infrequently adopted equations or data from previous models from another continent, or even laboratory, due in part to the timing and objectives of each region’s research programs. Notably, to our knowledge, CLIMEX has not been applied to North America alone (nor adopted by North American researchers), and non-CLIMEX bioclimatic envelope models have not been applied to Australia. Somewhat surprising is the absence of any specifically Asian model, despite the presence of *Rhipicephalus australis* throughout Southeast Asia (Guglielmone et al. 2014).

Significantly, most models of Australian *Rhipicephalus* connect to one another due to their common source: the CSIRO. Its 15-yr ascendancy (1973–1989) produced four primary *Rhipicephalus* models (i.e., TICK1, MATIX, TICK2, CLIMEX) and four secondary models (i.e., Sutherst et al. 1973, PICKUP, LARVS, STERHB). The few other researchers around the world who constructed *Rhipicephalus* models during this period had different goals (Smith 1983, Weidhaas et al. 1983) or models too simple to incorporate into the Australians’ existing models (Osburn and Knipling 1982, de la Vega and Díaz 1985*a*). Consequently, although Australian modeling studies acknowledged the existence of other *Rhipicephalus* models, they had no need to borrow from them.

Models in South America show a similar pattern, with most produced by five groups: Smith et al., CENSA/UH, EMBRAPA, CIGB, and Estrada-Peña et al. Unlike models in Australia and North America, South American models borrowed model concepts and structure more frequently, sometimes beginning with a preexisting model and reparameterizing it for South American conditions (Lodos et al. 1995, Saueressig and Honer 1995, Hernández-Arrieta et al. 2000). Most models in North America came from three groups: USDA-ARS, TAMU, and Estrada-Peña et al. This smaller number of sources hides a relatively large diversity in focus and structure of North American models.

As pioneers of a *Rhipicephalus* (*Boophilus*) modeling program (Sutherst 1993), CSIRO researchers appear to have had the right approach: First build simple models to explore different aspects of a problem, use them to generate testable hypotheses and identify needed data, and finally test the hypotheses or obtain new data with field or laboratory experiments. In some cases, they used field and laboratory results to improve previous models or to construct new ones, some of which they later integrated into pre-existing models. As Sutherst et al. (1979*a*) emphasized, "...the greatest value of this modelling approach lies in its ability to identify the key ecological and managerial questions that lead to improved pest control and to focus research and extension effort towards this end." Indeed, some tick data identified as lacking during development of BoopMod (Corson et al. 2004) were later provided by an Australian laboratory experiment (Sutherst and Bourne 2006).

Researchers in both Australia and South America had the ability to conduct experiments with live *Rhipicephalus* (*Boophilus*); in contrast, eradication of *Rhipicephalus microplus* and *Rhipicephalus annulatus* in the United States meant that few researchers in that country could do so (Popham and Garris 1991, Strey et al. 1991). The USDA-ARS Cattle Fever Tick Research Laboratory has generated much laboratory data about *Rhipicephalus* (*Boophilus*), but it has performed outdoor studies only in stalls or biosecure pastures. Consequently, most North American models based themselves on an amalgam of U.S. laboratory or Mexican and Australian field and laboratory data. Except for rough field observations before and during the U.S. eradication program, no field data exist to evaluate models of *Rhipicephalus* (*Boophilus*) populations in the United States. As a result, TAMU researchers evaluated their models with sensitivity analyses and comparisons with Australian field studies, which did not provide direct comparison with the scenarios simulated.

The reinstatement of *R. australis* as a sibling species of *R. microplus* (Estrada-Peña et al. 2012, Guglielmone et al. 2014) has spurred new ecological studies of *R. microplus* in South America (Canevari et al. 2016). It may also spur reconsideration of past model predictions and revision of existing models, especially those that used data from one species to represent the other species, or those developed by merging data from both species together. Although basic model structure is unlikely to change, models may require recalibration to represent the species or even local "variety" of *Rhipicephalus* (*Boophilus*) more accurately, depending on the modeler's question.

Ultimate use of these models has also varied. More than others, the Australians applied their models to cattle production systems in the field. Elder et al. (1983) were able to predict quantitatively effects of changing breed type in Queensland. In particular, the decision-analysis model of Elder and Morris (1986) appeared robust and detailed enough to support their management suggestions. Even a regional tick ecology program in Africa was based on predictions of Australian tick models (Sutherst 1987*b*). Other models helped determine appropriate pasture spelling and rotation periods and could be applied to other tick species. TICK1 was used to create the T3HOST model, and TICK2 also simulated two- and three-host ticks (Sutherst 1985). Models have been useful for walking the management tightrope between enzootic stability and instability/outbreaks of bovine babesiosis (e.g., Smith et al. 2000). South American researchers also used their models in a similar way, with de la Vega and Díaz (1987) using them to identify future research and Lodos et al. (2000) beginning to apply them to vaccine-related management decisions. Most models in North America, however, have remained untested theoretical constructs, serving mainly to identify the most important factors to vary in the next model, but some may be directly applicable in planning strategies to maintain eradication in the United States in the face of global change, including climate change (Pérez de León et al. 2012), which is predicted to expand habitat suitable for *Rhipicephalus* ticks to the north (Giles et al. 2014).

As Walker (2011) noted, complex mechanistic models may be too complex for management purposes. Models with fewer parameters to calibrate may be just as effective at predicting appropriate timing of management (Dye 1992). Sutherst (1987*b*) stated that models "offer an escape" from the "waste of resources" caused by isolated field research of the same parasite species in similar climates. Sutherst and Bottomley (1989) stressed the importance of using expert systems to disseminate the knowledge of the world's few tick experts and to compensate for a decreasing number of field experiments.

Thus, differing characteristics of *Rhipicephalus* populations within regions, and each region's organized reaction to them, have led to differences in ranking of important factors among models. For example, host resistance was important in Australian and South American models, in part because eradication was rarely an option. Conversely, larval longevity was important in North American models because it influences the success of pasture quarantines. Models also reflected changing research priorities over time. Acaricide resistance, which appeared in Australian models almost from the beginning, interested few North American researchers until *R. microplus* began to display acaricide resistance in Mexico. This alignment of research priorities may promote greater collaboration between Australian and North American *Rhipicephalus* (*Boophilus*) modelers in the future, despite the separation of *R. microplus* and *R. australis*.

LESSONS FROM THE PAST AND PERSPECTIVES FOR THE FUTURE

Perhaps the most important lesson emerging from 45 yr of *Rhipicephalus* (*Boophilus*) modeling on several continents is that a diverse suite of modeling approaches is necessary, given the wide range of scales (i.e., genetic to global) of *Rhipicephalus* biological, ecological, and management issues. Some models need less detail and accuracy in biological submodels because of their large spatial and temporal scales (e.g., global) or uncertainties in other submodels (e.g., encounter rate, human factors). Even when focused at different scales, however, models with similar purposes have converged over time to include most of the same important factors. More recent models of *Rhipicephalus* population dynamics, for example, include explicit representation of temperature and ambient moisture, both drivers of development and mortality rates. Similarly, bioclimatic envelope models calculate indices of temperature and ambient moisture, either directly, from weather data (Sutherst and Maywald 1985), or indirectly, from remotely sensed vegetation or geographic data (e.g., Giles et al. 2014).

Although from a theoretical point of view it seems trivial to conclude that model structure and level of detail depend on model purpose, in practice this lesson seems hard to apply or learn. Models do not arise by logical inference from data about the real system, and reasons for choosing one model structure over another are not found in the data themselves, but rather in ideas about how a model will help connect the data to other knowledge (Lander 2010). To decide how useful this connection is, that is, to evaluate the usefulness of a model, we must clearly identify (1) the purpose of the model, (2) the criteria the model must meet to be declared useful, and (3) the intended context for the model. Arguably, Rykiel's (1996) observation that the last two items are seldom specified for ecological models remains valid. Model context, often overlooked, embodies all model assumptions, especially those that are unstated and relegated to the system environment of the model. Dixon et al. (1997) argued that increasing the number of parameters in a model may increase its realism, but may reduce its interpretability.

Two of the most pressing reasons for developing a new generation of *Rhipicephalus* (*Boophilus*) models are to assess effects of global change (Pérez de León et al. 2012) on (1) tick eradication/management programs and (2) emergence/reemergence/expansion of tick-borne diseases. The scope of global change includes interactions among environmental, climate, social, political, and technological changes at multiple temporal and spatial scales. Global change influences ecological processes, which influence tick biology and ecology and consequently the epidemiology of pathogens transmitted by ticks (Reisen 2010, Tabachnick 2010).

Questions arise about which criteria to use to assess how well *Rhipicephalus* (*Boophilus*) models serve the purposes described above. We suggest that models must be able to generate appropriate spatial–temporal dynamics of both ticks and pathogens in response to changes in climatic conditions, landscape structure, and host-community composition. Current climate-driven GIS-based bioclimatic envelope models estimate potential changes in habitat suitability resulting from changes in climatic conditions and patterns of land use (e.g., see review by Walker 2011), and current mechanistic population dynamics models predict probability of tick persistence under given environmental conditions (e.g., Miller et al. 2012). Direct comparison of predictions of bioclimatic envelope models with those of mechanistic population dynamics models (e.g., Höner et al. 1993; Estrada-Peña et al. 2006*b*, 2014) appears useful.

It is now widely recognized that native wildlife serves as important reservoirs and dispersal agents of *Rhipicephalus* (*Boophilus*) ticks (Cançado et al. 2009, De Meeûs et al. 2010, Pérez de León et al. 2012). Indeed, *Rhipicephalus australis* in New Caledonia has adapted to parasitize Rusa deer (*Cervus timorensis russa* (de Blainville); Barré et al. 2011). In response, wildlife hosts are now explicitly represented in *Rhipicephalus* (*Boophilus*) models (e.g., Zeman and Lynen 2010, Estrada-Peña et al. 2014, Phillips et al. 2014, Wang et al. 2016).

Models of other tick species have been used to explore (1) the efficacy of novel approaches to tick control such as targeting acaricides at specific types of hosts (Wang et al. 2012), (2) effects of seasonal fluctuations in host densities and abundances of tick life stages on dynamics of vector-borne pathogens (Wang et al. 2015), and (3) effects of changes in host diversity and community composition on disease risk (LoGiudice et al. 2003). Development of analogous models for *Rhipicephalus* (*Boophilus*) would provide the ability to hypothesize specific cause–effect relationships, test their ability to generate the patterns of tick abundance and pathogen prevalence observed in the field, and simulate how these patterns might be changed by specific interventions in time and space, and in the tick life cycle.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1942/full