

# Meta-analysis, validation and application of fruit fly development times

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**Abstract** Tephritid fruit flies have been comparatively well studied because of the damage they cause to horticultural crops in affected countries. New Zealand benefits from this knowledge as it continues to exclude economically damaging fruit fly species. For example, fruit fly development models are used for biosecurity risk analysis and decision making during incursion responses. Here, the literature was searched for development times for three species of particular concern to New Zealand: the Mediterranean fruit fly, the Queensland fruit fly and the oriental fruit fly. The published data were re-analysed to fit development models to the different life stages and the generation time. The new models were then compared with previously published models for these species. The generation time models were found to give reasonably accurate predictions when validated against published estimates of field voltinism overseas. This paper presents the most comprehensive analysis to date of fruit fly development times and degree day models.

**Keywords** biosecurity, phenology, risk analysis, Tephritidae, voltinism.

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## INTRODUCTION

Fruit flies (Diptera:Tephritidae) include some of the most economically significant horticultural pests world-wide. New Zealand is naturally free of damaging fruit flies, and biosecurity authorities implement various systems to prevent introduction and establishment, including surveillance trapping (Acosta & White 2011). While all exotic tephritids are considered a threat to New Zealand horticulture, three species of particular concern are the Queensland fruit fly (Qfly), *Bactrocera tryoni* (Froggatt), the Mediterranean fruit fly (Medfly), *Ceratitis capitata* (Wiedemann) and the oriental fruit fly, *Bactrocera dorsalis sensu stricto* (Hendel).

Because of their significance to horticulture, fruit flies have been comparatively well studied

in infested countries, and New Zealand benefits from this knowledge in its efforts to exclude economically damaging species. For example, there have been many laboratory studies on the development times of fruit flies at different constant temperatures, and publication of a plethora of development models. These models can be useful both for risk analysis and for informing surveillance and eradication programmes (Nietschke et al. 2007), but it is not clear which models are the best nor how much natural variability in development times occurs within species.

Here, previously published data for development times of Qfly, Medfly and oriental fruit fly at constant temperatures

are re-analysed and used to predict voltinism (number of generations per year) in the field. These predictions are compared to published observations. The use of these models for New Zealand biosecurity is also discussed.

## MATERIALS AND METHODS

Development times at constant temperature were compiled from the literature, and new development models were fitted to the full data set available for each life stage of each species. Development models are usually fitted by least-squares regression as linear relationships between development rate (1/development time) and temperature, but this method may lead to misleading predictions, particularly at low temperatures (Kramer et al. 1991). Instead, non-linear regression (Brown 2001) was used to fit models directly to the data as  $d = q / (T - b)$  where  $d$  is development time in days,  $q$  is the total degree days required to complete development,  $T$  is temperature in °C and  $b$  is the base temperature below which development ceases. New Zealand is generally cooler than the native ranges of most fruit flies, and this method results in more accurate predictions for lower temperatures (Kramer et al. 1991). Variability was assessed as the 95% confidence interval around the fitted line, although this will underestimate the variability between individual insects because the data themselves represent the median result from a replicated experimental treatment.

To estimate generation time, the component models for eggs, larvae, pupae and pre-reproductive females needed to be scaled to a common base temperature  $b_c$ , which was the average of all the stages'  $b$  values weighted by their relative durations  $q$ . Models were refitted to the data as  $d = q_c / (T - b_c)$  and the resulting  $q_c$  values for each stage were added to estimate the overall developmental requirement. When raw laboratory data were unavailable, the stage models were re-scaled around a pivot temperature of 25°C (close to optimum for many fruit flies) as  $q_c = q \times (25 - b_c) / (25 - b)$  (Morris & Fulton 1970). This rescaling assumes that the original model gave the correct development time at 25°C

and recalculates the developmental requirement  $q_c$  from the adjusted base temperature  $b_c$ . This function could also be plotted in  $q$  versus  $b$  parameter space to indicate approximately equivalent models.

The new models were then validated as follows. Published observations of voltinism (number of generations per year in the field) were compiled, and daily maximum and minimum temperatures were interpolated for these sites from the nearest CliMond site (Kriticos et al. 2012). For each location, the development models were used to predict voltinism from the temperature data using the 4-step method (Kean 2013). Comparison between observed and predicted voltinism indicated how well the laboratory-based development models apply in the field.

## RESULTS

### Development models

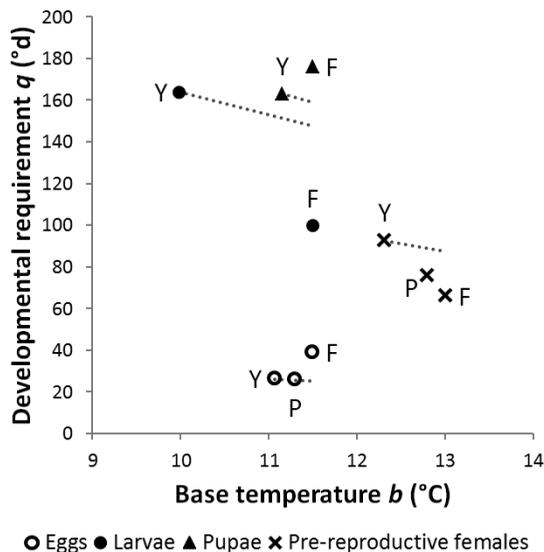
#### *Queensland fruit fly*

Surprisingly, no systematic experimental study of the development rates of Qfly in relation to temperature has been published. Pritchard (1970, 1978) gave data for egg development and the female pre-reproductive period, to which nonlinear models were fitted. Yonow et al. (2004) used these models and all other available data to derive development rates  $r$  for each life stage in the linear form  $r = m \times T - c$ , where  $m$  is the linear slope and  $c$  the y-axis intercept. Here, these parameters were recast using  $q = 1/m$  and  $b = c/m$ . The Australian code of practice (COP) for management of Queensland fruit fly (Anonymous 1996) uses values from an unpublished model by BS Fletcher of CSIRO, which differ considerably (Figure 1). Given that this model is not documented, Yonow's values were used: eggs require 26.2°d above 11.1°C; larvae 164°d above 10.0°C; pupae 163°d above 11.2°C; and the female pre-reproductive period requires 92.6°d above 12.3°C. Re-scaling to a common base temperature suggested a mean minimum generation time (egg to first egg) of 447°d above 11.0°C. In comparison, Meats (1981) suggested a nonlinear model for egg to first egg that approximates to 481°d above

10°C. Mean generation time (egg to median egg) was estimated from life table studies. At 25°C, Fitt (1990) estimated the mean generation time at 43 days; assuming an 11.0°C base temperature, the degree day requirement was  $43 \times (25 - 11) = 602^\circ\text{d}$ .

#### Mediterranean fruit fly

Considerably more data were available for Medfly (Figure 2). Egg development times from ten different studies (listed in Figure 2) suggested  $37.8 \pm 1.2^\circ\text{d}$  were needed above 10.0°C ( $df = 58$ ,  $R^2 = 0.978$ ). Data from ten studies, excluding results from sub-optimal hosts, suggested larvae required  $106.6 \pm 4.1^\circ\text{d}$  above 10.7°C ( $df = 39$ ,  $R^2 = 0.916$ ). Similarly, data from eleven studies suggested pupae required  $186.2 \pm 3.4^\circ\text{d}$  above 9.1°C ( $df = 75$ ,  $R^2 = 0.935$ ). Female pre-

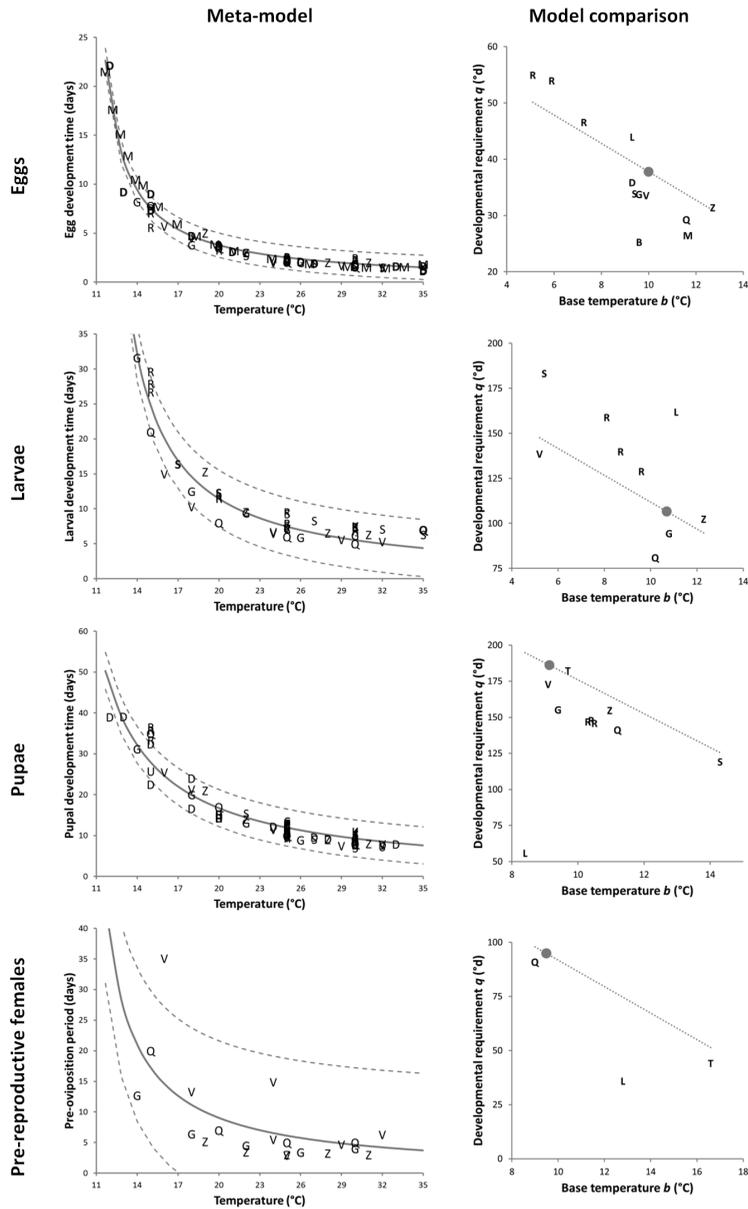


**Figure 1** Comparison of development parameters for Queensland fruit fly life stages. Parameter sources: P = Pritchard (1970, 1978); F = Fletcher (cited in Anonymous 1996); Y = Yonow et al. (2004). Dotted lines show equivalent development requirements estimated using a pivot temperature of 25°C; models appearing above the line suggest longer development times, those below the line shorter.

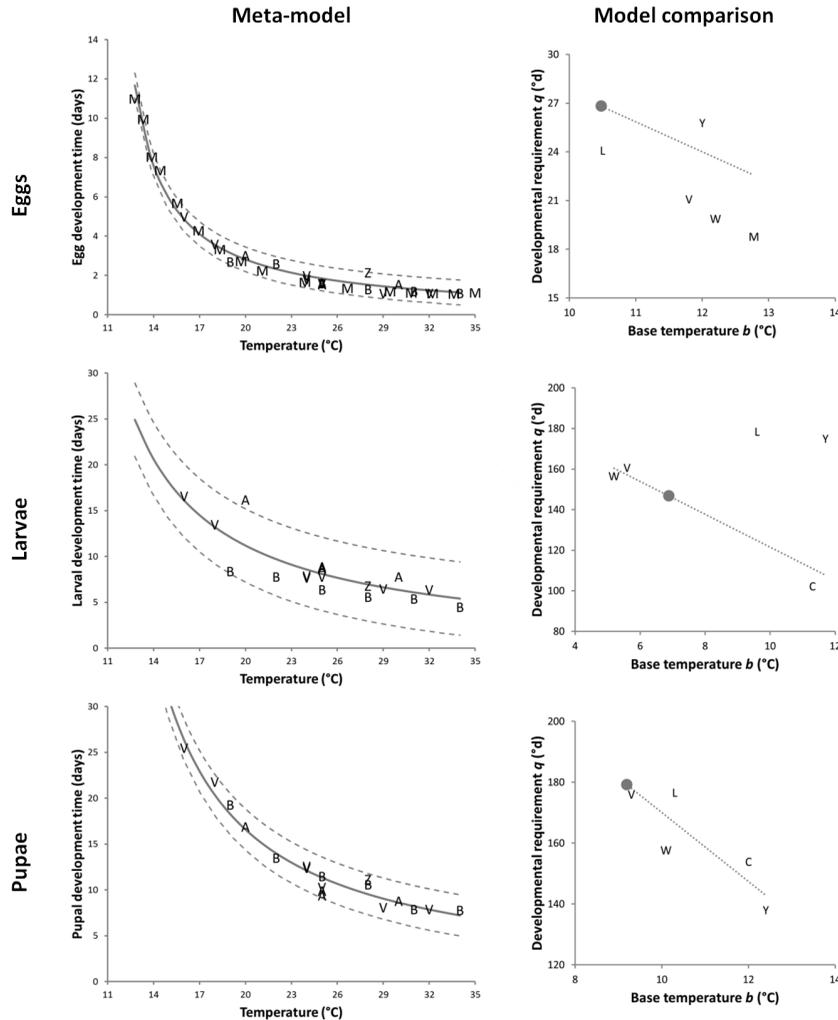
oviposition times were available from only six studies, and these showed substantial variability. In particular, the values measured from Hawai'ian populations (marked V in Figure 2) were substantially longer than those measured elsewhere. The model fitted in this case was  $94.9 \pm 12.6^\circ\text{d}$  above 9.5°C ( $df = 19$ ), but this has poor predictive power ( $R^2 = 0.424$ ). Refitting the models with a common base temperature suggested a mean minimum generation time of  $41.8 + 125.5 + 149.7 + 92.1 = 409.1^\circ\text{d}$  above 9.7°C for egg to first egg. This was comparable to the  $391.4 \pm 6.6^\circ\text{d}$  above 9.3°C ( $df = 8$ ,  $R^2 = 0.982$ ) fitted to egg-to-first-egg development times reported in two studies (Muñiz & Zalom 1997; Grout & Stoltz 2007). It was, however, substantially shorter than the mean generation time requirement of  $659^\circ\text{d}$  above 8.3°C ( $df = 30$ ,  $R^2 = 0.890$ ) fitted to results from five life table studies (Vargas et al. 1984, 1997, 2000; Krainacker et al. 1987; Papadopoulos et al. 2002).

#### Oriental fruit fly

Many of the studies of oriental fruit fly development were published in Chinese academic journals with a short English summary. Raw development time data were found in eight papers, and a further four papers published values for  $b$  and  $q$  in their English abstracts (these are listed in the caption for Figure 3). Models fitted to the raw data (Figure 3) suggested egg development requires  $26.8 \pm 0.6^\circ\text{d}$  above 10.5°C ( $df = 32$ ,  $R^2 = 0.986$ ), larvae require  $146.8 \pm 4.0^\circ\text{d}$  above 6.9°C ( $df = 18$ ,  $R^2 = 0.677$ ) and pupae need  $179.2 \pm 2.3^\circ\text{d}$  above 9.2°C ( $df = 18$ ,  $R^2 = 0.956$ ). Few studies reported pre-oviposition times and these were so variable that a fitted model had little predictive power ( $R^2 = 0.293$ ). Without a reliable model for the pre-oviposition period, the minimum egg-to-egg generation time cannot be estimated by summing the requirements of pre-reproductive stages. However, six life table studies (Vargas et al. 1984, 1997, 2000; Liu et al. 1985; Yang et al. 1994; Zhang et al. 2010) estimated mean generation times at different temperatures, which suggest a requirement of  $876 \pm 34^\circ\text{d}$  above 9.5°C ( $df = 18$ ,  $R^2 = 0.752$ ).



**Figure 2** Meta-analysis of development times for Mediterranean fruit fly life stages. Meta-model fits are shown on the left (data, solid line fit and dashed line 95% confidence range), and compared to other published models on the right. The meta-model is indicated by a dot with dotted lines indicating equivalent requirements around a 25°C pivot temperature; models appearing above the line suggest longer development times, those below the line shorter. Data sources: C = Carey (1984); D = Crovetti et al. (1986) and Delrio et al. (1986); G = Grout & Stoltz (2007); K = Krainacker et al. (1987); L = De Lima (2008); M = Messenger & Flitters (1958); P = Papadopoulos et al. (2002); Q = Duyck & Quilici (2002); R = Ricalde et al. (2012); S = Shoukry & Hafez (1979); T = Tassan et al. (1982) from Bodenheimer (1951); U = Quesada-Moraga et al. (2012); V = Vargas et al. (1984, 1996, 1997, 2000); Z = Muñoz & Zalom (1997).



**Figure 3** Meta-analysis of development times for oriental fruit fly life stages, as for Figure 2. Data sources: A = Liu et al. (1985); B = Yang et al. (1994); C = Chen et al. (2010); L = Luo et al. (2009); M = Messenger & Flitters (1958); V = Vargas et al. (1984, 1996, 1997, 2000); W = Wu et al. (2000); Y = Yuan et al. (2005); Z = Zhang et al. (2010).

### Validation of voltinism

Table 1 lists twenty locations where voltinism has been recorded, and Figure 4 shows the observed versus predicted values. Considering all species together ( $n = 21$ ), linear regression of observed versus predicted values (Piñeiro et al. 2008) suggested that the slope of the fitted line did not differ significantly from 1 and the intercept did not differ significantly from 0, but the root mean squared deviation of 1.7 generations

suggests there was considerable error. Thiel's partial inequality coefficients (Smith & Rose 1995) suggested that 85% of this error was not due to the slope or intercept. Similar results were obtained for the three species analysed separately.

### DISCUSSION

The current paper gives the most comprehensive synthesis and comparison of development times for these three fruit fly species to date.

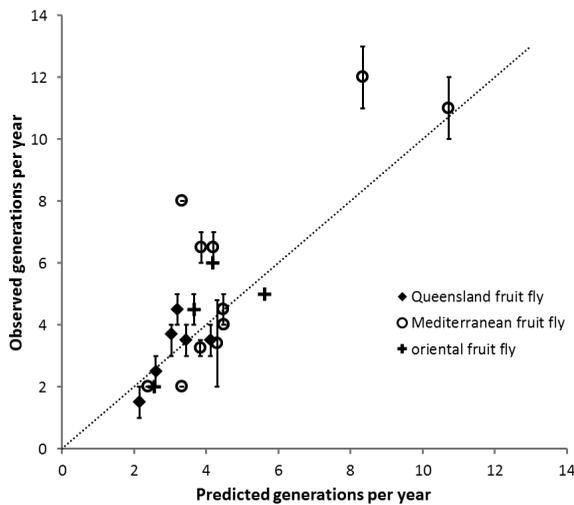
**Table 1** Observed voltinism of fruit flies at different sites compared with predictions from the meta-models. Predictions assume one generation of Queensland fruit fly requires 602°d above 11°C, Mediterranean fruit fly requires 659°d above 8.3°C, and oriental fruit fly requires 876°d above 9.5°C.

Location, country	CliMond site (lat., long.)	Estimated °d/year	Generations per year		Reference
			Predicted	Observed	
<b>Queensland fruit fly</b>					
Wilton, AU	-34.25, 150.75	1922	3.2	4 to 5	Fletcher (1974)
Melbourne, AU	-37.75, 144.92	1565	2.6	2 to 3	O'Loughlin et al. (1984)
Wodonga, AU	-36.08, 146.92	1826	3.0	3.7	
Adelaide, AU	-34.92, 138.58	2073	3.4	3 to 4	Maelzer (1990)
Sydney, AU	-33.92, 151.25	2478	4.1	3 to 4	
Orange, AU	-33.25, 149.08	1290	2.1	1 to 2	Muthuthantri (2008)
<b>Mediterranean fruit fly</b>					
Madiera, PT	32.75, -16.92	2198	3.3	8	da Silva Vieira (1952)
Honolulu, US	21.25, -157.75	5495	8.3	11 to 13	Hagen et al. (1981)
Paris, FR	48.92, 2.42	1573	2.4	2	
Rome, IT	41.92, 12.42	2769	4.2	6 to 7	
Santa Clara, US	37.25, -121.42	2528	3.8	3 to 3.5	
coastal high plains, GT	14.08, -90.92	7068	10.7	10 to 12	Eskafi & Kolbe (1990)
elevations >2000 m, GT	15.42, -91.08	2836	4.3	2 in 5 months	
Adelaide, AU	-34.92, 138.58	2961	4.5	4	Maelzer (1990)
southern FR	43.58, 1.42	2191	3.3	2	Cayol & Causse (1993)
Thessaloniki, GR	40.58, 22.92	2952	4.5	4 to 5	Papadopoulos et al. (2001)
Aydin, TR	37.92, 27.92	2546	3.9	6 to 7	Karagoz et al. (2009)
<b>oriental fruit fly</b>					
Hekou, CN	22.58, 103.92	4917	5.6	5	Jiang et al. (2001)
Ruili, CN	24.08, 97.92	3655	4.2	6	
Kunming, CN	25.08, 102.75	2230	2.5	2	Ye & Liu (2005)
Wuhan, CN	30.58, 114.25	3204	3.7	4 to 5	Han et al. (2011)

Previous authors (e.g. Vargas et al. 1996) assessed similarities between development models by comparing the developmental requirements  $q$ , but this is uninformative when the base temperatures  $b$  differ because  $q$  depends on  $b$ . More often, authors compared models in terms of  $b$ , but without reference to  $q$ . Here, for the first time, a pivot temperature (Morris & Fulton 1970) has been used to compare fruit fly development models in terms of both  $b$  and  $q$ , which allowed identification of which models predict relatively longer development times and which shorter. The choice of pivot temperature, 25°C, matched the typical median temperature used in laboratory studies of fruit flies, but in New Zealand's temperature climate there may be more interest in development times at lower temperatures.

Because of the way they have been fitted, the new models for Medfly and oriental fruit fly should perform better than previous models at the lower end of the suitable temperature range (Kramer et al. 1991).

Some authors (e.g. Tassan et al. 1982) refitted models to development data from other studies, but this is the first time models were fitted to collective data from a range of Medfly and oriental fruit fly studies. This analysis also indicated variability between genotypes, rearing conditions and study methods. For example, conformity between different studies of Medfly or oriental fruit fly egg development times (Figures 2 and 3, top left) suggests higher confidence in the new models. Larval development times were more variable, probably



**Figure 4** Observed versus predicted voltinism for three fruit fly species (Table 1). Vertical error bars indicate published ranges of generations per year; the diagonal dotted line shows where model fit is perfect.

reflecting differences in host substrate suitability (Carey 1984; Krainacker et al. 1987), but pupal development was more consistent. The greatest uncertainty was associated with the duration of the female pre-oviposition period, which varied widely between studies and between treatments within studies, suggesting that factors other than temperature may influence this life stage.

There is some confusion in the literature about what constitutes “generation time”. In some cases the mean egg-to-first-egg time is used, as in the Australian COP for Qfly (Anonymous 1996). This might be considered a minimum generation time, and for the species examined here, that value was considerably shorter than the egg-to-median-egg time that constituted the mean generation time obtained from life table analyses (e.g. Fitt 1990). Validation of the egg-to-median-egg models suggested that they are appropriate, on average, for estimating voltinism in the field although the predictions for some sites were inaccurate. The low precision (i.e. spread around the regression line in Figure 4) might be partly attributed to the temperature data used for validating voltinism being only approximate in time and space.

Insect phenology models are widely and routinely used in pest management and, more recently, in biosecurity management (Nietschke et al. 2007). These models can inform risk analysis by suggesting climate suitability, voltinism and potential impacts in invaded areas (Kean & Kumarasinghe 2007). For example, Meats (1981) estimated the voltinism of Qfly across Australia and concluded that the low number of generations possible in southern Victoria constrained populations from reaching damaging levels by summer’s end, and speculated that Qfly would only cause significant damage in areas that can sustain at least three generations per year. In New Zealand, temperatures suggest that this would only be the case from the Hauraki Plains north (J.M. Kean, unpublished data). Potential voltinism has also been used as an index of climate suitability in more complex assessments of spatial and temporal biosecurity risk (Magarey et al. 2011).

Other uses for phenology models in biosecurity include trace-back (assessing the potential circumstances of introduction) and trace-forward (forecasting subsequent growth and spread), both of which may be important aspects of incursion responses (van Havre & Whittle 2015). A development model run on local temperatures may suggest when an insect invader arrived, and which life stages should be targeted by surveillance. For example, international guidelines for proving area freedom from fruit flies recommend that surveillance should be maintained for up to three generation times after the last confirmed detection (FAO 2006), whereas the Australian COP for Qfly uses one generation (calculated as the egg-to-first-egg generation time) plus 28 days (Anonymous 1996). The development models derived here were used to estimate these dates for the current Qfly incursion in Auckland (J.M. Kean, unpublished data).

#### ACKNOWLEDGEMENTS

I am grateful to Dave Voice (MPI) for useful discussion, and to Craig Phillips, Alison Popay, Sue Zydenbos and an anonymous reviewer for helpful feedback on the manuscript. This work was funded by the Ministry for Primary Industries

RFP 15184 and by AgResearch's contribution to the Better Border Biosecurity (B3) cooperative research programme (b3nz.org).

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